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THE

VEGETABLE INDIVIDUAL,

IN ITS

RELATION TO SPECIES.

BY

DR. ALEXANDER BRAUN,
Professor of Botany in the University of Berlin, &c. &c.

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The Vegetable Individual, in its relation to Species, (Das Individuum der Pflanze in seinem Verhältniss zur Species,—Generationsfolge, Generationswechsel und Generationstheilung der Pflanze); by Dr. ALEXANDER BRAUN, Professor of Botany in the University of Berlin, &c. &c. Berlin, 1853.* Translated by CHAS. FRANCIS STONE.

PART I.—INTRODUCTION AND HISTORY.†

IN Organic Nature the two principal phenomena, in which the shifting scenes of Life are unfolded, are individual development and individual propagation. Through them the intricate course of Nature, and its living chain of organized beings, are refreshed and renewed. Every new generation seems to bring back the old form; still, to the investigator who looks deeper into the graves of the past, a slow, but certain, progress reveals itself even in this apparently identical succession. If nature is to be for us something more than a labyrinth of varied and intricate phenomena; and if, in the apparent disorder, the hidden threads of the connection are to become visible, we must first of all separate and compare the different spheres of life, placing them higher or lower, according to their rank. The starting-points, which nature offers for such a purpose are, the *Individual* and the *Species;* whose reciprocal relations, however simple they may at first appear, when followed out to particulars lead to difficulties which

* From the Transactions of the Royal Prussian Academy of Sciences, for 1853.
† I have omitted the author's brief introductory remarks.—*Transl.*

demand an accurate examination.* From the Botanist such an examination is particularly demanded; as the vegetable ideal presented to us by the science in its earlier stages has been obscured by conceptions obtained from the animal kingdom having been transferred to Botany, though based upon the mistaken assumption that plants possess the same independent individuality as animals, the same organs with equally well-defined functions, and the same mutually dependent relations of the vital activities. And the investigations of late years, forsaking the old views more and more, have arrived at no well-defined conclusions, and, particularly as regards vegetable individuality, seem to lead more to negative than to positive results. After all, this should not surprise us; for even a superficial investigation shows relations in plants which will hardly harmonize with the common conceptions of individuality, and which require a careful review.

In the whole realm of organic nature, we know of not a single species of which any one individual is a perfect representative: on the contrary we see each species adding generation to generation, by multiplying the individuals in time and space, until its day has ended, whether from internal or external causes. In this particular, the species resembles the individual itself; having its allotted age, though measured by days of a higher order, and its appointed cycle of life,—in which the individuals appear as members occupying a certain time and place,—resembling the successive relative forms through which the individual passes. For the organic individual does not manifest itself in one single permanent form, but in a succession of forms, now gradually connected, now broadly interrupted; and these last, especially in plants, may attain to an independence, which gives them the character of a subordinate species. To this analogy between individuals and species it may be objected, that, in most cases, a very remarkable metamorphosis is connected with the successive forms of the individual, while within the sphere of the species the consecutive members continue to have essentially the same

* Should any one be inclined to doubt that the nature of the vegetable individual needs a futher discussion, I would beg him to turn to the latest works on Botany and compare the passages which treat of the plant's individuality. I take *Kützing's Grundzüge der phil. Botanik* (2nd Part), as we have a right to demand from a work that lays claim to philosophical development, a fundamental discussion of this subject, since it is the ground-work of the whole science. The first two paragraphs under the heading "*Das Pflanzenindividuum als Organismus*," read as follows: "By individual we here mean a single vegetable body not organically connected with a similar vegetable body. Vegetable individuals have the power of developing the general phenomena of vegetable life by themselves, unassisted by any other individual of the same species. It is the nature of an organism to consist of members. . . . The possession of members is the first, as well as the most essential condition of the existence of the vegetable individual." Not one of these assertions is true of vegetable individuals, either in the broader or the narrower signification of the term. To say nothing of the connection, in which the individuals appear which are successively developed by shoot-formation, the coalescence of stocks which were originally sepa-

character.* But, however important this fact may be, still we may assert of the individual as well as of the species, that it completes the cycle of its existence in a succession of subordinate generations, while, on the other hand, we may affirm of the species, that like the individual, it exhibits a determinate cycle of development.† In comparing the processes of propagation with the process of the formation of the individual, cell-formation, which lies at the foundation of both, reveals the intimate connection which exists between the small and the great spheres of development; while the numerous cases which admit of a double explanation (since they may be ascribed with almost equal justice to the inferior cycle of development of the individual, or to the superior one of the species) establish the close relationship of both. The above-mentioned circumstance, that the cycle of development does not present as graduated a progress in the species as it does in the individual, seems to suggest that the most reliable view of the analogy between the species and the individual is that in which the species is not compared with the whole cycle of the individual's successive development, but with the *single steps* of the metamorphosis (which of course has its own subordinate members), and in which the species itself is regarded as an inferior "momentum" of a still more comprehensive cycle of development; but to determine this would lead us too far from our subject.‡ In a word, the relation of the individual to the species is that of an inferior cycle of development to a superior: the individual is a *member* of the species. However, although they are under one and the same specific law, all the members of the species are not identical: a single member only represents the idea of the species more or less incompletely; and certain members, or series of members, are thus reciprocal complements. The regular relations here brought to view will form the principal subject of the present investigation. But we must first carefully determine the sphere of the individual. The individual shall not and may not be considered by itself: it must be viewed

rate is no rarity. Are the pines of a pine-forest no individuals because, as Göppert has shown, they are connected with each other by their roots? Do the filaments of *Zygnemæ* cease to be individuals when they copulate. Are the cells of *Hydrodictyon* and *Pediastrum*, originally separate, no longer individuals when they have joined themselves into a net, or a star? To refute the second assertion, we may refer to diœcious plants; to refute the third, we refer to the one-celled Algæ and Fungi, a part of which, at least, are of such a character that we can by no means ascribe to them an *organisation* in the usual acceptation of the term. However, we may regard it as an improvement, that *Kützing's Grundzüge* treats of the vegetable individual at all; for the earlier manuals do not even mention this important subject, but commence their account of plants with descriptions of the root, stem and other organs, or, as it has been preferred of late years, of the cells and vesicles.

* Those of the forms and properties, which persist through the successive generations, determine the species. *Link: Grundlehren der Kräuterkunde*, vi, p. 11.

† The species is an individual of a higher rank (higher power). *Link*, l. c., p. 11.

‡ Cf. the Author's work on *Verjüngung* (1849), note to p. 344.

in the successive generations to which it belongs. This succession may be similar or dissimilar, simple or complicated by divisions, continuous or graduated by cyclical changes. It is by this that the phenomena of fissiparous and alternate generation may be explained. It is only by a consideration of these relations that the nature of the individual itself, as a subordinate sphere of the species' development, can be rightly comprehended, and that the single individuals in their worth and importance, in their relations to each other and to the whole realized cycle of the species, can be understood.

Preliminary remarks on Vegetable Individuality: different views in regard to it.

We must determine what constitutes the vegetable individual, before we can investigate its relations to the whole cycle of generation of the species. But it is this determination itself which presents so many difficulties; and these difficulties become the greater, the further we push our investigations. Individuality in plants seems as obscure and ambiguous, as in animals (at least in their higher orders,) it appears clear and simple; so that, as Steinheil remarks, it escapes us just when we are upon the point of seizing it ;* and investigators might even conclude that we can realize no other individuality than that which is manifested in the totality of the species. The first obstacle to our comprehending the vegetable individual as a single sphere of conformation, as a morphological whole, is the disconnected and separate character which obtains in the most heterogeneous modifications of vegetable organisms. For no where in the vegetable kingdom do we perceive that indissoluble connection, and those pervading reciprocal functions, which in the animal kingdom we are accustomed to associate with the idea of an individual organism. Nevertheless, by starting from a comparison with animals we get an apposite point of departure for a comprehension of the plant's individuality. Among the higher animals, the individual appears as a member of a race produced by sexual generation; and this very test may be applied to plants, except in the very lowest forms, to which sexual generation does not apply at all, or not positively. Without at present discussing the question whether the vegetable individual thus conceived is truly analogous to the animal individual, we may here state, that this conception carried out to its consequences, involves the assumption that all the plant-stocks produced, not by sexual generation, but by any mode of vegetable division, are not individuals, but only parts of the primary individual to which they owe their origin; as Gallesio has

* "Dans chacun de ces organes nous nous croyons au premier aspect sur le point de saisir l'individualité normale, et partout elle nous échappe." *Steinheil: De l'individualité végétale* (1836), p. 9.

in fact contended.* Botanists have often asserted that it is the individual† alone, which is reproduced by slips (branches, buds, tubercles etc.), and their opinion coincides with this view. Still, how are we to distinguish plant-stocks of such an origin, from those derived from seeds? The former take root, ramify, blossom, ripen their fruit and seeds, just as the latter do, so that in a physiological sense they are complete individuals.‡ For example, let us cast a glance at the weeping-willow (*Salix Babylonica*). It is well known that this tree, which was originally brought from the banks of the Euphrates, is always propagated by slips; for with us it never bears seeds—not because our climate is unfavorable, but because in our gardens there is no fructifying male tree.§ According to Loudon (*Arboret. Brit.*), the weeping-willow was sent to England in 1730, by a French merchant named Vernon. It was planted in Twickenham Park, whence it spread rapidly over England and the continent. The tree, from which the first slips that were brought to Europe were taken, was most probably a cultivated one itself, raised from a slip. However this may be, could the descent of all our weeping-willows be traced, it would undoubtedly lead us back to a willow, a female willow, grown in its native country from a seed. And so, on this account, we are to regard all the beautiful weeping-willows of our gardens and our cemeteries—and surely they are perfect trees—not as individual stocks, but as the *disjecta membra* of a primary trunk, now hidden in mythical darkness! In other cases this pri-

* *Gallesio: Teoria della riproduzione Vegetale* (1816), a work, which I am sorry to say I have not been able to consult myself. *Huxley* (upon Animal Individuality, in the Ann. and Mag. of Nat. Hist., June 1852), holding corresponding views, regards all the animals which spring from an egg by non-sexual increase, as *one* individual, or, as he expresses it, as a representative of the individual by successive coëxisting separable forms;—regards as such, for example, the sum total of all the *Aphides*, produced in successive generations, by non-sexual increase, from the first "nurse" which sprung from the egg. If we assume with *Bonnet* that one nurse encloses one hundred young Aphides in the tenth generation (and according to *Kyber* they often reach even a higher number) the series would amount to much more than a billion (1,010,101,010,101,010,101). Those who regard sexual reproduction as the criterion of individuality must admit this as a perfectly legitimate consequence of their view.

† "Gemmæ individuum continuant cum semina speciem propagent." Link: *Elem. phil. Botan.*, ed. II, v. i, p. 332. "Continuant," in antithesis to "propagent," cannot be mistaken. Again Endlicher und Unger: *Grundzüge der Bot.*, p. 85, say, "In these cases (i. e. when the buds drop off) the bud-formation is a true propagation, by which the individual is multiplied; though we must distinguish this mode of propagation from that of generation, by which the species is reproduced." Here the meaning is obvious, though the expression is perfectly paradoxical; for how can we imagine that the individuals are multiplied without the species being reproduced? I have elsewhere attempted to show what is here meant, by representing non-sexual propagation as a propagation *subordinate* to the cycle of sexual reproduction (cf. *Verjüngung*, pp. 26, 27).

‡ In many cases the experienced gardener can distinguish them, but certainly not in all; in some the difference is very remarkable: e. g. in *Araucariæ* raised from branches.

§ This has the advantage of avoiding the disagreeable seed-down. For the same reason, it is said, in China they cultivate the male tree only.

mary trunk is known with perfect certainty. It can be proved by history that many hybrids and varieties have been produced in one single exemplar; though they now ornament our gardens far and wide, having increased by means of slips, as they do not bear seeds. This was the case of the famous *Cytisus Adami*, which sprung, shortly before the year 1825, from the mingling of *C. purpureus* and *C Laburnum*. The single parent-stock, preserved in the garden of the celebrated Adam in Paris, has long since disappeared; but its scions and scions-scions, have grown up into fine trees in half the gardens of Europe.* In the view just stated, they all form but one individual! To support such a view, its partisans adduce the fact of certain individual particularities being preserved (in diœcious plants especially the gender), when propagated by slips. In general this is true, and for practical gardening, e. g. for the cultivation of the finer kinds of fruit, of the greatest importance; but exceptions are not rare; among which the well known re-division of *Cytisus Adami* into its two primary stocks is one of the most striking and remarkable. In our gardens the rule is that from slips the weeping-willow produces female trees; still some exceptions may be noted here. Napoleon's grave in St. Helena is shaded by a weeping-willow, which has become the subject of scientific discussions. It was supposed to belong to a species (*Salix Napoleonis*) indigenous to that Island; but Loudon's exhaustive researches show that it is descended from our weeping-willows, one of which was carried from England to St. Helena in 1810. Branches of this *Salix Napoleonis* were brought back to England, and to the astonishment of botanists they bore *male* flowers. Since up to that time no male weeping-willows had been seen in England, a change of gender must have been produced through vegetative increase. A similar case has also occurred in Germany. In the Grand-ducal Gardens at Schwetzingen there is a weeping-willow which, although a descendant from the common parent tree of all European weeping-willows, has changed its gender to such a degree that we not only find on it the most heterogeneous stages of transition from female flowers to male ones, but on many branches purely male catkins are produced.† Besides these cases, a curled variety of weeping-willow *Salix crispa* or *S. annularis* of the gardens, is known; which, as it is a mere garden plant, has probably been produced by slip-propagation. If it be true that we sometimes obtain varieties with hanging branches from several kinds of trees by grafting the slips inverted, we should have one of the most remarka-

* Cf. *Verjüngung*, pp. 337 and xi. In another place I shall communicate the history of this hybrid, which has since been investigated.

† This tree was first observed by *C. Schimper* in 1827. Some remarks upon it may be found in *Spenner's Flora Friburgensis*, vol. iii, p. 1061.

ble examples of the production of a singular peculiarity by non-sexual increase. But even if such exceptions did not exist, and if in every case a series of peculiarities which are extinguished in seminal propagation were continued by grafting, yet we cannot perceive how we can seriously refuse an individual existence to such stocks as these, produced, it is true, by non-sexual propagation, but still completely separated externally, developing in different places and under the most dissimilar relations, and exhibiting subordinate differences indefinitely, though with certain similar characteristics. But if we were to make any concessions on this point we should be carried irresistibly on to others.

Most of the modes of non-sexual propagation thus far considered agree in this particular; that some *shoot* of the plant, whether it be undeveloped (eye, bud), or developed (branch, sucker, layer, &c.), is separated from the parent-stock by natural development itself, or by artificial means. As the nature of the separable part is not changed by the separation, it is no great step to attribute individuality to the shoot, (or as it is commonly called, the bud,) even when it is not separated from the stock. Each single plant-stock could then be no longer regarded as an individual in the usual meaning of the term, but as an united family of individual shoots;—a view which seems to be of high antiquity; as passages are found in Aristotle* and Hippocrates†, which are interpreted in this sense. In later times, this view has been more or less, advocated, especially by De la Hire,‡ Linnæus, Darwin§, Batsch, Goethe, Röper, Schleiden‖ and others.

But, even in this narrower view of vegetable individuality, the same difficulty meets us; for the shoot itself is divisible, and new stocks may be produced by its parts: i. e. by the members of the

* Cf. *Wimmer: Phytologiæ Aristotelicæ Fragmenta*, §§ 23–28, 66 et 113. I cannot discover that explicit acknowledgment of the individuality of shoots or buds, which is said by Schultz (*Anaphytose*, p. 24) to be found in Aristotle, either in Schultz's quotations, or even in Wimmer's complete collection of the passages in Aristotle referring to plants. It is true that Aristotle repeatedly speaks of the divisibility of plants; says that separated parts of plants may continue to exist; that on this account many trees may spring from a single source; that many plants are propagated by slips (ἀπὸ σπαραγαμάτων ἀποφυτευομένων), and by lateral bud-formation (τῷ παραβλαστάνειν) e.g. the bulbous plants; but he does not state his opinion of the parts which develop after such a separation, and explains the phenomena in general, by saying that the vegetable soul of plants (θρεπτικὴ ψυχὴ) is simple in actuality, (ἐντελεχεί) though multiple in capacity (δυνάμει).

† According to *Moquin-Tandon: Teratologie*, p. 5.

‡ *Hist. de l'Acad. Roy. des Sciences*, 1708, p. 233. De la Hire regards all the branches as new plants proceeding from hidden ovules. Myriads of these ovules, he thinks, exist between the bark and the wood; more or less of them come to maturity, according to circumstances.

§ *Darwin: Phytologia* (1800), p. 1. "If a bud be torn from the branch of a tree, or cut out and planted in the earth . . . ; or if it be inserted into the bark of another tree, it will grow and become a plant in every respect like its parent. This evinces, that every bud of a tree is an individual vegetable being, and the tree therefore is a family or swarm of individual plants . . . ."

‖ I shall consider the views of these authors more at large in the next section.

stem and its leaf or leaf-whorl.* Besides, the several members of the shoot are not contemporaneous creations, but, developing successively out of and over each other, they constitute a successive generation, composed of divisions each of which repeats essentially the same form, each of which may be compared to the embryonic plant originally developed in the seed, and consisting of its stemlet with one or two leaves (cotyledons). Thus the shoot itself came to be regarded as a *succession of individual vegetable members*, built up one above the other, like the stories of a house. The earliest traces of this view may be found in *Darwin's Phytologia*;† it was developed at a later period in various ways and with various modifications: e. g. by Agardh‡, Engelmann,§ Steinheil‖ and Gaudichaud¶—the last of whom calls the member of the shoot elevated to the rank of an individual vegetable being, "the phyton," and ascribes to it not only a stem and leaves, but even a root, by which he imagines it is connected with the preceding phytons, as the first phyton (the embryonic plant) is connected with the ground. Steenstrup** and Forbes†† employ a similar view for their comparison of alternate generation in plants with that in the lower animals.

But this restriction of vegetable individuality could not stop here; for even the members of the shoot, the "phyta" or "stories," are themselves too complex organisms not to present subordinate divisions, which, like the whole member possess a certain independence, and under certain circumstances may even give birth to new stocks. Although botanists have attempted to view the petiole as the lower part of the leaf,‡‡ or, vice versa, the leaf as the upper part of the petiole,§§ (so as not to be compelled to divide the phytons of the structure themselves into rel-

* I adduce this point in connection with the history of the views held by botanists in regard to vegetable individuality, in the terms in which it has been usually expressed; further on I shall show that this view needs qualification. The individual members of the stem cannot expand into a new stock by direct development, like the separated shoot; they have this property only by being connected with a lateral sprout, by means of the eye which they bear, or have the power of producing. This view naturally brings us back to the shoot as the individual.

† P. 9; where even the single well-defined stem-members of different herbaceous plants are described as so many buds, and hence as so many individuals.

‡ *Agardh: Essai de réduire la Physiologie végétale à des principes fondamentaux*, 1829, (Ann. des Sci. Nat., tom. xvii, p. 86).

§ *Engelmann: de Antholysi*, (1832) p. 12.

‖ *Steinheil: l'Individualité dans le regne végétale.* 1836.

¶ *Gaudichaud: Recherches sur l'Organographie, la Physiologie et l'Organogénie des Végétaux.* 1841.

** *Steenstrup: On alternate Generation* (1842), p. 128. As this important little work may be supposed to be in every one's hands, I refrain from quoting this interesting passage.

†† *Forbes: On the Morphology of the reproductive system of Sertularian Zoophytes, &c.*, Ann. and Mag. of Nat. Hist., v. xiv, (1844), p. 385.

‡‡ *Ernst Mayer: die Metamorphose der Pflanze und ihre Widersacher.* Linnæa, 1832, p. 401.

§§ *Hochstetter: Aufbau der Graspflanze.* (Würtemberger Jahreshefte, 1847 and 1848).

atively independent members) this much at least is certain (and it is the important point here), that each of these two parts is capable of producing new growths by itself, yes, this capacity is enjoyed even by different determinate or casual parts of either member. It is well known that the leaf of *Bryophyllum* produces sprouts in every notch on its edges, while on the other hand, caducous leaves of many bulbous plants (e. g. *Eucomis regia*, according to Hedwig, *Ornithogalum thyrsoides* according to Turpin)* produce new plants in the form of bulblets on any portion of the whole of the upper surface. The petiole itself under certain circumstances, has the power of producing the so-called adventitious buds, not only on the portions determined by the position of the leaf (leaf-axil), but sometimes on any other portions; a power enjoyed by the root in many cases. Hence parts of plants, otherwise most dissimilar, when they contain cambium, may have the power of reproducing the plant.† This is the foundation of the *Schultz-Schultzenstein-ian* doctrine of *anaphytons;* viz., those vegetable members "which, even when separated from the plant, continue to live, bud, and develop,"‡ and which are hence regarded as the individuals proper, as the true elementary forms or morphological elements; and it is by various combinations of these that the organs (commonly so-called), root, stalk and leaf, are formed, by the repetition of which the whole plant is built up and indefinitely renewed.

But where are the limits of the anaphytons? How shall lines be drawn to include all the buds of the root, stalk and leaf, from which new formations may spring? Aub. du Petit Thouars§ who had already developed doctrines similar to those of the anaphyton-theory, attempts to draw the line between individuals by means of the cellular tissue, regarding every vascular bundle as an individual, since it has in itself, and independently of all others, the means of its growth, its preservation, and the reproduction of new bundles. But it is difficult to perceive how, in such a view, the labyrinth of anastomosing bundles, (not less complicated in the majority of petioles, than in most reticulated leaves,)

* Cf. *Treviranus: Pflanzenphysiologie*, where several examples are adduced.

† Aristotle himself says that plants possess the power of reproducing "stalk and root" in every one of their parts. (πανταχῇ γὰρ ἔχει καὶ ῥίζαν καὶ καῦλον δυνάμει. Vit. long. et brev. c. 6, p. 467).

‡ *Schultz: die Anaphytose* (1848) and, *System der Morphologie* (1847). The passage quoted is taken from his later work, Verjüngung im Pflanzenreich (1851). The remark made above, when treating of the members of the petiole, holds good here. The so-called Anaphyta can by no means grow into new plants themselves; on the contrary, the new plant is produced as a germ, which is not identical with the anaphytons.

§ *Essais sur la végétation considérée dans le développement des bourgeons* (1809) cf. e. g., p. 174. "C'est donc le bourgeon en qui réside toute l'énergie végétale; aussi le regarde-t-on depuis longtemps comme un individu . . . . . D'après les principes que j'ai développés dans mes précédens mémoires, il faut aller plus loin, car je crois que chaque fibre végétale est un *Individu*, puisqu'elle a en soi, indépendamment des autres, les moyens d'accroissement, de conservation et de réproduction."

can be disentangled and resolved into separate individuals and why the same independence and the same rank should not be allowed to the parts of the vascular bundles. And how shall we regard the lower plants, which have no fibres at all? If our conclusions are to be anything more than mere arbitrary assumptions, we must go still farther; and we shall find no halting-place till we reach *the cell*, the true seat of every renovation in the plant, the starting-point of all non-sexual increase,* as it is of sexual propagation.† The cell has a better right to be considered as the vegetable individual than any other subordinate member of the plant; when connected with other cells it still continues to be an independent sphere of formation, sharply defined and, in youth at least, completely isolated.‡ Before the universal law of cell-formation was known, and before botanists had succeeded in reducing all the elementary organs of plants to cells, Turpin hit upon the idea of seeking the vegetable individual in the cell; though his views did not rest on as solid a foundation as Schleiden's assertion that: "in a scientific point of view, the cell is the vegetable individual."§

The most reliable authorities have agreed that new cells can never be formed externally to, but only within, other cells already formed,¶ so that cell-multiplication must be regarded as a propagation, while all the cells of the mature plant must be regarded as the progeny of the first embryonic cell. Besides, each and every plant is at first a cell; and there are single-celled plants in the strictest sense of the term, in which the first formation of new cells is that destined to reproduction; i. e.: the germinating cells or spores.** Again, there are other plants in which the cell-generations contained between the first generation (which

* Earlier investigations into the origin of adventitious buds had made it probable that, in its formation, each new shoot arises from a single cell. The first convincing proof of this fact, was given by *Hofmeister* (Vergleichende Untersuchung u. s. w. der Coniferen, p. 94), in *Equisetum*. The propagating cells on the foliage and edges of the leaves of liverwort, which develop into new plants, have long been known. The spores of the Cryptogamiæ belong here, as they are cells originating and developing non-sexually.

† Pollen-cells, and the embryonic utricle and germinating cells,—as well as those of the archegonium of the higher Cryptogamiæ.

‡ Malpighi himself (Anatom. Plant., 1675), calls cells utriculi, or sacculi, though he distinguishes the wood and bast-cells as "*fibræ*," the vascular cells as "*fistulæ*" and the cells containing milky sap as "*vasa specialia*." As early as 1805, Link (Römer's Archiv., iii, p. 439), had expressed himself very explicitly in regard to the isolated position and the independence of cells: "Quaevis cellula sistit organon peculiare, nullo hiatu nec poris conspicuis præditum in vicina organa transeuntibus. Conspicies non raro cellulam rubro colore tinctam inter reliquas virides."

§ *Schleiden: Grundzüge*, 1te Aufl., 1842, vol. ii, p. 4, [Eng. trans. (1849), p. 127 T.]

¶ Cf. *Schleiden: Grundzüge*, i, p. 267 [Eng. trans. p. 103 T]. "The process of the propagation of cells, by the formation of new cells in their interior is an universal law in the vegetable kingdom." *Mohl: Anat. und Phys. d. veg. Zelle*, 1851, p. 53. "Cell-formation in plants takes place only in the cavities of older cells, not between or upon them." *Schacht: die Pflanzenzelle* (1852), p. 47. "The formation of new vegetable cells always takes place in the interior of cells already formed."

** E. g.: *Ascidium*, *Chytridium*, *Codiolium* (a genus lately discovered in Heligoland) *Sciadium*, *Hydrodictyon* (the last two with "colonial formation").

sprung from spores) and the last (itself returning into spores) separate from each other, so that all the cells belonging to one cycle of vegetable development are segregated, and live completely independent of each other.* The importance of the cell as an individual seems to be decided by these facts; that of the entire plant, as a superior whole composed of individual cells, seems to be settled, and a firm foundation for the doctrine of vegetable individuality to be gained. But let us try to obtain a clearer view of some of the most important of these facts. The view which regards all cell-formation as a process of reproduction rests upon observations of the formation of free daughter-cells (blastidia) in the contents of the mother-cells (matrices),—the so-called *free*, or *endogenous*, cell-formation. Schleiden, who discovered this process, and Karsten† the most decided and original of his followers, regarded endogenous formation as the universal law of cell-formation. By this view the whole doctrine was turned in a wrong course, from which it could only be gradually recovered by the discovery, or rather the farther investigation, of another mode of cell-formation, which Nägeli designated as "wandständige," Unger as "merismatic," and Mohl as "cell-formation by division of the primordial utricle." But even at this day the misconception caused by generalizing the view that new cells are formed *within* old ones, has not been entirely removed. I have already‡ called attention to the fact that cells are divided which have no cell-wall, which is often the case among the Algæ.§ In several genera in which numerous spores are formed in one mother-cell, its entire contents first divide into two parts (the so-called daughter-cells) which, without first secreting a cell-wall, immediately divide again into two; and this process may be repeated over and over,‖ according to the number of spores which are to be formed (8, 16, 32, &c). In the second and subsequent divisions there is no formation of new cells *in* old ones, of daughter-cells *in* mother-cells, and hence no reproduction, in the sense of one or more individuals being produced *in* an old one. The *entire* mother-cell is converted into two filial cells; the filial cells are nothing but the mother-cell divided. And this is essentially the case in every cell-formation by division: for the wall of the mother-cell (within which the division gener-

* Many Palmellaceæ, Desmidiaceæ, and Diatomeæ. Cf. *Braun: Verjüngung*, p. 132, et seqq.

† H. Karsten, (*De Cella Vitali*, 1843,) emphatically rejects every mode of cell-formation by division and by sprouting, and asserts that every cell originates at its first appearance as a dot-like utriculus; regarding all formations found in the contents of the cell as cell-brood.

‡ Cf. *Verjüngung*, p. 245.

§ E. g.: Protococcus (viridis), Characium, Pediastrum, Ulothrix, Enteromorpha, Ulva, etc. during the process of spore-formation.

‖ Nägeli (*Monocellular Algæ*, p. 28) calls such cell-generations "transitory generations."

ally takes place) certainly is not the living mother-cell, but merely its cast-off garment, its perishing shell. Cell-formation by division (called the "merismatic" or "wandständige") is that which obtains through the whole realm of vegetative development; while free cell-formation occurs only in fructification. Thus, the same phenomenon, which, regarded as endogenous cell-formation, seemed so favorable to the importance of the cell as the vegetable individual, when more justly comprehended only brings us back to the divisibility of the vegetable organism, repeated in the most heterogeneous spheres. But still more: even the cell whose contents are not converted by division into new cells, but remain simple, presents phenomena which can hardly be reconciled with their view by those who regard such a cell as an individual, isolated in space and independent in time. In the genera *Vaucheria*, *Bryopsis*, *Caulerpa*, and other related Algæ in the family of *Siphoniæ*, we find such cases, examples of the most extraordinary kind of cell-formation. The single cell, which forms the vegetable organism of these plants, has in fact a development which may continue indefinitely. Certain parts of the elongated stem-like cell shoot forth into branches which lengthen by an independent terminal growth, without separating from the cavity of the maternal trunk by any partition. The principal trunk of the cell is either creeping, with an indefinite terminal growth though dying off from behind (*Caulerpa prolifera*),* or it is upright and deciduous, while the sucker-like branches, club-shaped at the ends, and filled with a denser contents, are perennial (*Vaucheria tuberosa*).† In both cases the branches separate from the dying trunk, closing up at the bottom; and thousands of new trunks may thus be produced without any proper cell-formation. Thus the cell leads us back to the point from which we started at the tree; and, as we could not refuse individuality to the ramifications of the tree, neither can we refuse it to the ramifications of the cell. Hence we cannot regard the cell as an absolutely single being, completely isolated and indivisible. Shall we penetrate still further into the anatomy of the cell itself, in the hope of possibly finding a valid vegetable individual? All that we discover here is, first, the vesicles, spherules and granules in the contents of the cell (amylum, chlorophyll and other pigment-vesicles, spherules of fat and, finally, the granules of the viscous cell-contents, whose chemical nature it is difficult to determine); and secondly, the fibres, which compose the cell-membrane according to the old view advanced by Grew and lately revived by Meyen‡

* Cf. Nägeli's important paper on this plant (Zeitschrift für wissen. Bot., i, p. 134), especially the exposition of the above-mentioned relations beginning p. 158.

† A new species from the vicinity of Lake Neuenberg in Switzerland, remarkable for its purely furcated ramifications, with constrictions at the bottom of the branches, as well as for the club-shaped suckers at the ends.

‡ *Meyen: Pflanzenphysiol.*, i, p. 45; answered by Mohl, in his *Vermischte Schriften*, p. 314.

and J. Agardh.* These parts, it is true, have often been regarded as the elementary forms† of plants, or their primary "individualized" bodies;‡ the attempts, however, to represent them as the true and real vegetable individuals are not numerous; and they astonish us by their daring rather than entice to imitation. Turpin, who commenced by considering plants to be composed of different kinds of individual cells, which he compared with various lower plants (especially the Algæ-genera *Protococcus* and *Conferva*), afterwards expanded his views, so as to regard the cells themselves as individuals of a second rank; while he considered the true primary individuals to be the granules of the cell-contents, from which, in his opinion, the cell (cell-wall) is formed by agglomeration.§ Mayer of Bonn, basing his theory upon molecular motions, considers the smallest granules of the cell-contents as individuals possessing animal life (biospheres) which build up plants for their dwellings. "Like hamadryads these sensitive monads inhabit the secret halls of the bark-palaces we call plants, and here silently hold their dances and celebrate their orgies."‖

Farther than this we cannot go: if we did we should have to leave *specific* vegetable life, and, instead of investigating its most minute spheres of formation, the visible cells, vesicles, granules or monads, turn to the invisible *individua*¶ of brute matter, so as to consider plants as phenomena of appellant and repellant, coherent and incoherent atoms. If we must understand by an in-

* *J. Agard: de Cell. Veg. fibrillis tenuissimis contexta* (1852). Notwithstanding the importance of the author's new investigations, they still need a more searching examination, as some points directly contradict well-ascertained facts, e. g.: the direct transition of the fibres from the outer to the inner layers of the cell-wall. The whole theory of the formation of cells by the uninterrupted growth of fibres cannot be admitted in view of the undoubted independence of the formation of tbe cell-wall from the contents. Mohl is certainly right in regarding the fibrous division and divisibility of many cellular tissues as a mere structural relation of the membrane (which in other parts is continuous); and he thinks it depends upon the peculiar mode of agglomeration of the molecules. As such molecules of the cell-wall are invisible, I think it preferable to regard it as dependent upon a regular change of the relations of density.

† *Kützing: Phil. Bot.*, i, p. 125, 129, does not regard the cell as the elementary form of plants, but as a complicated structure itself, and preceded by many other more simple forms, which he comprehends under the name of "molecular tissue," and which, he says, present in themselves many lower vegetable forms. Plants which are not even cells!

‡ *Unger: Grundz. d. Anat. u. Phys. der Pflanzen*, p. 4. The cell is represented as the "elementary vegetable organ;" but the vesicles, fibres and granules within it are further distinguished as very minute, "individualized" bodies.

§ *Turpin: "Sur le nombre deux,"* (Mém. du Musée, xvi, 1827, p. 305): "Ainsi des individus globuleux, rapprochés simplement contigus, forment la membrane de la vésicule Individu du tissu cellulaire, le filament Individu du tissu tigellulaire, et la membrane cuticulaire Individu. Des agglomérations de ces derniers constituent les Individualités, provénantes des bourgeons développés, et enfin, celles-ci achèvent *l'Individualité composée* d'un arbre."

‖ *Mayer: Supplemente zum Lehre vom Kreislauf* (1837), p. 49. I am acquainted with Mayer's views through Meyen's Pflanzenphys., ii, p. 256.

¶ Cicero calls the atoms "Individua."

dividual, a being perfectly simple and indivisible, this is our last refuge, in which we may indeed reach an individual, but not a *vegetable* individual; for this would then be identical with the material individual common to all corporeal existence. But, even if we could give up all hopes of a specific vegetable individual, doubt would still linger round these physical individuals; for even the existence of the universal primary particles of bodies,—the material individuals, the atoms,—is not conclusively established. No eye has seen them; we do not even think of considering them as objects of direct perception; we only accept them as an hypothesis, to eke out our theories of motion and of chemical affinity, and to enable us to compute their relations. The question might easily be asked, whether the same phenomena may not be as well explained by assuming the continuity, expansibility and penetrability of matter. However this may be, the question concerning the existence of atoms certainly lies beyond the limits of botanical investigation; and if the existence of vegetable individuals depends on this question, the botanist must despair of proving it. Thus the question at which we have now arrived is this: can we speak of individuals in botany? and this is identical with another: are plants mere products of the operations of matter (i. e., of a substance self-moving, uniting and separating by an innate force), and hence non-entities, or mere phenomena resulting from, or produced by, the blind forces of nature; or may we ascribe to plants an independent existence in nature, notwithstanding their connection with the external world?

If what we call plants are nothing but complex chemical and physical *processes*, then we can no longer speak of their individuals and species in the sense the words usually bear; for the mere phenomena of the operations of the primary substance, which have no other efficient principle than the forces of this substance, cannot be regarded as self-existent beings, or as peculiar (specific) kinds of these beings, or as single (individual) modifications of them. This is, in fact, the result towards which the later physiological investigations are hastening, grounded on the positive results of investigations in the physical sciences. Even vegetable physiology cannot resist this tendency of science, although it struggles more or less against these conclusions.* The operations by which plants, and all organic beings, form and preserve their organisms, were formerly ascribed to peculiar vital forces; but the physiology of our day would recognize in the vital functions of the organism the same forces by which the processes of inorganic nature are perfomed. Thus physiology becomes

* Even Schleiden, the most prominent and most decided of the representatives of this tendency, seeks to counterbalance the deadening effects of the purely materialistic view by an æsthetic one (Die Pflanze und ihr Leben; last lecture: d. Æsthetik der Pflanzenwelt).

physics and chemistry, or, according to the usual conception of the physical and chemical processes themselves, the "mechanics" of organic nature in the most comprehensive meaning of the term mechanics. And thus the life of the enchanter is unveiled, who had seemed to be the immediate cause of his own works; the lofty partition-wall between organic and inorganic nature falls, and one common foundation is laid for investigating all material processes in every realm of nature. This important result is reached: the existence of the higher orders of natural phenomena, which had been regarded as the peculiar realm of Life, is referred to the same natural causes (the same material substance and the same kind of forces) by which the lower orders, those of "inanimate" nature, have their being and perform their functions. Still further conclusions may be attempted, and it is in the nature of scientific progress that these attempts should be made. As physical forces seem to be everywhere indissolubly connected with matter, and as a fixed regularity displays itself in their operations, men were found bold enough to consider the totality of natural phenomena as the result of original primary substances, coöperating with determinate forces, according to the laws of a blind necessity;—a natural mechanism revolving in its endless orbit.*

Though this view seems to explain all the phenomena of nature from one principle, in fact it precludes any real explanation of them, that is when exlusively applied to their solution. That which is eternally necessary can only be conceived as eternally carried out; and thus any real event becomes an absurdity. If the "mechanical" (physical and chemical) forces of nature are necessarily active, then if any motion is to take place, the first impulse, the proximate cause, cannot be explained by the nature of the motion; it must be another principle above necessity; and this is true not only of nature as a whole, but also of every particular motion in nature as well. Thus not only the first impulse, but the universally apparent final cause, remains an inexplicable riddle in the doctrine of blind necessity. Hence the insufficiency of the "physical" theory, compared with the "teleological"† is peculiarly obvious in the realms of organic nature, where the

* As far as concerns Natural History these views are developed, e. g.: in both of Mohlschott's works: d. Physiol. des Stoffwechsels in Pflanzen u. Thieren, (1851), and d. Kreislauf des Lebens (1852); in the last mentioned work we find such sentences as these: "The miracle of nature is the interchange of matter, the first-cause of physical life," p. 83. "Creative omnipotence means the relations of matter," (p. 258). "The hinge round which the wisdom of the present day is turning is the doctrine of the interchanges of matter," (p. 363).—The doctrine, that the universe is the play of attrahent and repellant atoms, belongs, after all, to the "wisdom" of the past, professed by *Democritus* and *Epicurus*.

† Cf. *Schwann: Microscopische Untersuchungen* über die Uebereinstimmung in der Structur u. d. Wachsthum d. Thiere u. Pflanzen, (1839), especially p. 221–225; on the other side, *Eschricht d. Physische Leben*, (1852), in sections ii and iii.

final cause of each particular life appears so distinctly. The advocates of the physical view perceive this; but they explain the fitness of means to ends in nature as a whole, and in its individual parts, by supposing matter, with its blind forces, to have been created by an intelligent being.* But we can regard this as a germ of an explanation only in proportion as it is also granted, that the intellect of the Creator lies not only behind and without nature and her processes of development, but that, as if incorporated in nature, it is taken into the destiny of each created being, in proportion to its individuality. But this, again presupposes the admission of a substantiality of nature fit for such an hypothesis;—a substantiality not grounded on mere matter, like a blind force; but which, on the contrary, must comprehend matter as subordinate to itself, and must realize itself through matter:—an assumption which modifies the physical view essentially, and would seem to be a modification of some ideal, or teleological theory.

Without underrating the great importance, which the physical view possesses for vegetable physiology, still we must confess that we cannot find in it the key to a conception of vegetable individuality: for, after all, this must be sought for, not in the external conformation, but in the essence of the plant, determined from within. This leads us from the last negative results to an historical view of the attempts at a positive explanation.

It is evident from the foregoing review that, if we would not give up all hope of conceiving plants as *beings, realized in individual conformations*, we must not allow so great and decisive an importance to the external divisibility of their organism as has been usually done. We must seek a decision in the essential concatenation of all the steps in the plant's development forming one whole, according to one idea. This is the tendency of the concluding remark of Nägeli, to which he is lead by the relations of growth and propagation in *Caulerpa*; when he says that indivisibility of form is not an element essential to individuality, —which, indeed must be constructed upon a new, and somewhat less material a basis. Link calls attention to this same unity, which is expressed in the whole development of the plant, and which forms the essence of its individuality, in the following true words: "We cannot recognize an individual unless we are convinced that it remains the same in different periods of its existence."† Now the question is just this: how can we perceive

* "The fitness of means to ends, in every organism, even a superior degree of this individual fitness, cannot be denied; but in this (the physical) view, the cause of the fitness does not consist in the fact that every organism is produced by an individual force tending towards a certain end, but, like the cause of the fitness of means to ends in the inorganic world, that matter is the creation of an intelligent being." Schwann, l. c., p. 221, and, in almost the same words, p. 224.

† *Link: Elem. Phil. Bot.*, Ed. ii, p. 11.

such a oneness of essence amid these changes of form and material? How do we perceive that, with all its divisibility, the plant remains after all really one and the same individual?

Every development presents a succession of phenomena, which, while they present themselves in a regular order, also show unmistakably a point of departure, an end, and a course between the two advancing after a fixed plan, and which indicate a common internal principle.* They point to an internal vital principle,† common to the whole succession;—to a principle which must be conceived of, not only as an idea which guides the whole process, or as a force determining the specific type of this plastic succession, but also as a living essence, comprehending the idea as its internal determination, and the force as the means of its realization;—an essence which precedes and shapes the external existence; as intentions precede and determine acts.‡ If, in ac-

* *Du Petit-Thouars*, l. c., p. 284: "L'individu est un être dont toutes les parties sont subordonnées à un principe unique d'existence." *Link, Elim. Phil. Bot.*, ed. ii, p. 3. "Nos individuum vocamus, quod ab uno eodemque principio interno determinatum est, ad idealem potius quam ad realem respicientes divisionem."

† *Spring: Ueber d. Begriffe v. Gattung, Art u. Abart*, (1838), p. 55. "It is this indwelling principle which makes the individual; and in natural history, every body is an individual in as far as it really exists as a single being, whose existence is determined by a peculiar indwelling vital principle." Spring afterwards distinguishes the *systematical* and the *physiological* individual: in the former one moment of the development is comprehended, in the latter the whole metamorphosis. The physiological individual comprehends an assemblage of forms, which might be regarded by a casual observer as so many systematical individuals.—Still, a true systematick must protest against such a purely subjective distinction of systematical and physiological individuals. However much the embryos of mosses resemble Confervæ, or the larva of an insect resembles a worm, a true systematick will not separate the young individual from the developed one; and genera which are founded upon our ignorance of their successive development, as *Protonema*, *Lepra*, *Sclerotium*, etc., must be given up by the systematist himself. True, we shall be called upon at a later point in this inquiry to decide, whether a sphere of development which really belongs to the individual can present itself to us so divided that the divisions themselves attain to the importance of subordinate individuals.

‡ Aristotle describes the internal essence of plants as a "plastic soul," (θρεπτικὴ ψυχὴ, τοῦ ζῶντος σώματος αιτία καὶ ἀρχὴ). Cf. *Wimmer: Phytol. Arist. frag.*, c. iii, de pl. vita atque anima. The charge of anthropomorphism has been made against such a view, which attempts to conceive of nature as a chain of essences, both in the reciprocal relations of her forces, and in her internal developments; but, if man himself is a member of nature, if he is the highest member in the order of natural beings, that member which presents the most complete unison of all the phases of life in nature,—then all his knowledge of nature must be connected with his knowledge of himself. However meanly we may estimate this knowledge at the present stage of psychological science, still it is sufficient to assure man of his own "ego." And if man is justified in regarding himself as a human being, by analogy he is justified in regarding his relations, the animals, in the same manner, as animal beings; plants as vegetable beings; and every single animal, every single plant, as an individual being (even though included in a higher entity). To attain a unity of idea in Natural History, man must apply this idea farther down in the scale of nature, and must regard minerals, even the elements themselves, as beings of their own kind. But the materialist will reply: individual beings are only the elementary substance: all other beings, so called, are formed by a temporary composition and coöperation of these. But who has seen these elements of chemical combinations, as *elements*, or has proved their existence in any way? But even if they should exist as such, is it not

cordance with this idea, we regard external development as the revelation of the internal essence, which exhibits its purport in the processes it undergoes in connexion with the world without it, and whose realization is thus produced by a determinate sphere of activities, necessary for such a realization, then, *vice versa*, we may infer the essential unity of each particular sphere of development, from the complete unity of the functions relating to this realization. This leads us to the attempts made at a physiological determination of the vegetable individual. The usual definition, and one entirely in accordance with the physiological point of view, is that an individual is a perfect representative of the character of the species, possessing all the functions necessary to the continuance of the species. Now if we would conceive of a physiological individual, in the broadest meaning of the term, we should certainly be compelled to demand that our conception should be such as to exhibit not only single phases, but all the phases of the specific life during its entire develop-

conceivable that a higher being should include the lower beings? We say: hydrogen and oxygen form water; but it would do as well to say, water forms itself out of hydrogen and oxygen. The elements do not form the plant; the plant forms its body out of the elements. We may declare both these views to be hypotheses; but of hypotheses that is preferable which is nearest to man,—I would almost say, most necessary to man's nature, when he proceeds from the data of his own existence. Shall the elements have a stronger claim to be acknowledged as real existences than man himself? Or will any one say that it is a more daring hypothesis to assume that man thinks; that brutes move themselves; that plants themselves produce the determinate form of their organism, than to suppose that elementary substances in their connexions and coöperations produce the phenomena of thought, voluntary motion and typical conformation? But after all, is it not true that the elementary substance is everywhere present? that without it none of the phenomena just mentioned can occur? Certainly, this is so; the higher stages cannot be realized without the lower, which enable them to exist; but these higher stages can never be explained by, and comprehended in, the lower. No one, as yet, has shown even the shadow of a possibility of explaining, from the things themselves merely, why the elementary particles form a mineral kingdom, a vegetable kingdom, an animal kingdom, and man. And why do they not fulfill their task after an eternal immutable manner, since such a fulfillment is one of their necessary, eternal, and immutable properties? Why have they succeeded in composing man only in the most recent geological epoch? Why have they not from eternity produced in man's brain the theory of their actions, and thus, in accordance with their eternity, eternally manifested and glorified themselves? The most industrious investigations into the relations of the physical world promise us a deeper insight into the regular connexions of all the parts of nature; into the cunning mechanism, which carries on and upholds all natural life. Still a key to the interior of this structure, and an admission to the essence of plastic nature in her operations, cannot be found by our investigations if, by presumptuous hypotheses, they debar us from the higher realms of development, especially those of organic nature and of human life. Flesh and blood are hypotheses; but mind is truth, says a well known writer; and Des Cartes could find a proof of his own existence and of that of the world around him in his mind alone. It would be a strange contradiction, if the investigation of the most distant realms into which the human mind can penetrate should rob us of what is nearest and surest, the intellectual *ego* itself, the starting point of all investigations. But he who has not recognized the foundations of the spiritual world in nature itself, must of consequence deny their existence in man, if he would not lose, in an inexplicable dualism, the hope of obtaining coherent views of nature.

ment; that it should realize all the capabilities of the specific being, and thus present to us the whole plan, the whole destiny of the species. If we examine the preceding conclusions from this point of view, it will be evident that single cells cannot be such individuals; for, although the whole construction of the plant and all the functions of its life are carried on by means of the cells, still, viewed as a connected whole, the cells are only single stones, single elements, in the great mechanism of the organism. Any single member of a plant (as the internode and leaf) corresponds no more to such a physiological individual than does the cell; for plants undergo their metamorphoses in their successive members; and the various processes of their preservation, reproduction and propagation are connected with the various steps of these metamorphoses. Nor can it be the shoot; for that usually does not embrace all the steps of the metamorphosis; besides, the functions are variously distributed in the shoot; and in many cases, this takes place for the reciprocal completion of the functions. Besides, whatever is characteristic in ramification and in growth depends upon the combined shoots, and without these it is impossible to conceive of trees, for instance. Then we come back to the whole plant-stock? Nay, farther; we cannot stop at the plant-stock; for the single stocks are far from being perfect representatives of all the phases, and tendencies of the specific life. I would refer to the division according to gender, or the modes of fructification, which is often made in botany; the diœcious and triœcious,* relations, and farther, to the varieties, especially to those which do not possess essential organs and functions, which belong to the species as such; e. g.: those varieties which never bear blossoms (Ball-acacias), or which never produce fruit (congested blossoms), or which never perfect seeds (currant-grape, cultivated bananas and bread-fruit trees). Besides, no stock is exactly similar to another: we ascertain only the limits of the possible relations of the specific form by a comparison of many stocks. As in animal physiology the solution of the problem of the life of many animals depends upon their social relations (societies composed of couples or of flocks, or of self-governing states), so in vegetable physiology it depends upon characteristic physiological traits whether plants live single and dispersed, or in societies. For example, in considering the life of turf-mosses we must determine whether they grow in great sods or in carpets; and of grasses, whether they form meadows; or of trees, forests. Even the relations of geographical distribution, which are discovered by a comparison of all the stocks, depend upon the physio-

* Triœcious plants are exceedingly rare among Phanerogamiæ (Ceratonia, some kinds of Rhus), but are more common among the Cryptogamiæ; perhaps we may add the Floridiæ. In *Polysyphanio violacea* I have found three kinds of stocks mixed, and in the same stage of development in the same place: (upon the same thread in *Chorda Filum*).

logical character of the plants: plants of sensitive and inflexible constitutions are found only within narrow limits; while plants of adaptive and pliant constitutions are more widely distributed, become migratory plants, and by degrees spread over almost all parts of the earth, if their seeds possess the necessary properties. From these considerations, and many others which might be adduced, it is obvious that there are no determinate limits to a purely physiological conception of the vegetable individual; and that we may expand the definition of the individual until it coincides with that of the species itself.

How then can we steer a middle course, between the morphological view, which results in indefinite subdivision, and the physiological, which ends in indefinite expansion? The physiological view has shown that none of the divisions or spheres of formation, which have been regarded as the individual ones, fully realizes the idea of the species; and that each needs the others to render this idea complete. The morphological view has shown, in the same manner, that there are subordinate and comprehensive spheres of development, none of which exhibits complete independence, since all appear in unequal degrees, as more or less perfect members of the entire succession of the specific development. If we would discover the individual under such circumstances, we must not demand of it all that belongs to the species; for this is *completely* represented only in the totality of the individuals, not in any single individual. We must answer this question: Which member of the graduated potential series in the sphere of development subordinate to that of the species deserves *preëminently* the title of individual? And we shall be compelled to reply: That which exhibits the most complete independence and definiteness. Good use has decided in regard to man (and the higher animals), and it justifies itself by the fact, that what is usually termed an individual undoubtedly possesses great organic independence: and this is true both of its subordinate spheres (i. e. the members of the organism, down to the cells) and of those by which the individual is comprehended (family, state, race, etc.). By means of comparison and analogy, the signification of the more doubtful spheres of development among the lower animals and plants may receive some new light from such a view. I propose to attempt this in the second part of this Investigation, but now I will only subjoin a few general remarks.

In the conception of individuality, there are two elements; that of multiplicity, and that of unity. Each development exhibits multiplicity; but this multiplicity is not equally subordinate to the unity in every development. The more complete this subordination, the more perfect is the individuality; for it is only this subordination to the unity which binds up the multiplicity of the conformation into an indivisible organism. The less com-

plete the subordination, the more perfect will be the independence of the parts, and the more indefinite will be the individuality of the whole. If we apply this view to plants, whatever is dubious in our conception of vegetable individuality will be explained. Successive development, we may say, is the peculiar nature of plants, which, beyond the power exhibited in the process of formation and propagation, possess no higher vital power; while in animals the process of the formation of the body appears only as an operation preparatory to its connection with a higher vital activity. For animals, in addition to their powers of external manifestations, have a power of internal vital comprehension, which expresses itself in the life of the soul (by which animals possess an internal centre, from which the organism is governed and regulated). It is the soul alone which connects in indivisible unity, and for reciprocal services the products of the plastic power, and gives to the organism of animals the character of a definite individuality. Among plants the case is different: plants in their operations are active solely in one direction, externally—are split up so to say in the process of external conformation, so that the parts appear less connected, as compared with the plant as a whole more independent, and more divisible among themselves. Thus the vegetable organism is a *dividual*, rather than an individual; a multiplicity* rather than an unity; i. e. a whole whose parts hold the same relation to each other as individuals to each other, but which present spheres as indivisible as the whole itself. This is the doctrine of the *relative*† individuality of plants, which Steinheil has especially noticed. According to this doctrine, different orders of vegetable individuals, as it were different powers of individuality, are distinguished. In the same manner DeCandolle‡ distinguishes the cell-individual (*l'individu cellulaire*, in which he has been preceded by Turpin); the bud-individual (*l'individu bourgeon*, after Darwin); the slip-individual (*l'individu bouture*); the stock-individual, or the vegetable individual (*l'individu végétal* penes quem est jus et norma loquendi); and the embryo-individual (*l'individu embryon*), which, in accordance with the meaning in which Gallesio used the term, comprehends all that proceeds from one germ, even if multiplied by division. Since the

* "Planta est multitudo." *Engelmann: de Antholysi*, p. 12.

† *Steinheil:* l. c., especially p. 4 and p. 17: "Les végétaux ne peuvent arriver à l'individualité absolue; ils se presentent à nous dans un état, qu'on peut désigner par le nom d'individualité relative; ce qui distingue cette partie de la création du règne minéral, où l'individualité est nulle, et du règne animal, ou elle est presque toujours absolue."

‡ *DeCandolle: Physiologie Végét.*, p. 957. The author does not attach much importance to his division, as he says he has assumed it for convenience of expression, and to avoid the usual confusion of language. His son Alphonse DeCandolle considers it quite an arbitrary matter which part of the plant we call the individual: "Les végétaux sont évidemment des êtres composés: mais jusqu' où veut-on les décomposer, pour que les élémens s'appellent des individus? C'est une chose arbitraire, qui dépend de l'idée par laquelle on se laisse dominer" (after Steinheil, p. 6).

slip-individual is essentially the same as the bud-individual (i. e. shoot-individual), we have four degrees of individuality, in which at least one more might have been easily inserted, between the cell and the shoot-individual, i. e.: the member or "story"-individual (Gaudichaud's *phyton*). With this view Schleiden's division is connected: he distinguishes the cell as the plant of the first order; the shoot as that of the second, which he calls the *simple* plant (a term borrowed from C. F. Wolf, who used it in the same sense); the whole stock as that of the third order, which he designates as the *composite* plant By a searching investigation into the shoot, I shall endeavor to decide whether all these relative individuals can be considered *individuals* with the same justice; or whether, after all, one of them does not deserve the title preëminently, corresponding to the animal individual. In either case Gœthe's words may be applied with perfect justice to plants and their individuality:

> Freuet euch des wahren Scheins,
> Euch des ernsten Spieles;
> *Kein Lebendiges ist Eins*
> *Immer ist's ein Vieles.*

Herder, in speaking of the works of the Creator, says: "Every one of Thy works Thou makest *one* and perfect, and like itself alone."

This sentence presents the other aspect of existence, by which the multiform is one; and every unity in the one-sidedness and incompleteness of all single manifestations, is after all a perfect whole. These words lead us to the internal essence of things, referring us at the same time to the primary ideas, which Nature comprehends and realizes in Life.

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THE VEGETABLE INDIVIDUAL

IN ITS

RELATION TO SPECIES.

*The Vegetable Individual in its relation to Species;** by Dr. ALEXANDER BRAUN.—Translated from the German by CHARLES FRANCIS STONE.

PART II.†

As I attempted to show in Part I, whatever seems arbitrary and indefinite in the existing views of what constitutes the Vegetable Individual has its ground in the nature of plants themselves, which, in their realization are resolved into a plurality which they are not capable of reducing to as complete an unity as animals are. As we ascend in the natural kingdoms, individuals increase in importance, until they reach their most perfect independence in Man. Hence, if we would appreciate them justly in the lower departments, in which their character is less definite, we must try to comprehend the less perfect structures by starting from the more perfect ones: to appreciate vegetable individuals we must start from a comparison of animal individuals.

* Das Individuum der Pflanze in seinem Verhältniss zur Species,—Generationsfolge, Genrationswechsel und Generationstheilung der Pflanze, by Dr. A. Braun, Professor of Botany in the University of Berlin, &c. &c.

† For Part I, see Number for May, 1855.

From this point of view we perceive at once that the cell cannot be regarded as the proper individual in plants, otherwise it would have to be considered in the same manner in animals. Cell-formation is a property common to plants and animals: but in animals it appears far more obviously as a subordinate element in the organization of the whole body, than it does in plants; since the animal cell, in most cases, is not so independent, nor so determinate, nor so permanently isolated as the vegetable cell. For this reason, too, it is rarer to find the animal cell considered as the proper animal individual, although *Schwann* has shown that animal cells are analogous to vegetable cells and may be as justly considered individual organisms as they. Yet as mere *curiosa* we might adduce the somewhat similar assertion of Gaillon, that "men and animals are properly masses of Infusoria;" and Oken's doctrine of generation, "a synthesis of Infusoria," might, perhaps, be interpreted in the same sense. The "stories" of the axes, the internodes with their leaves, might claim to be compared with the animal individual with more justice than the cell, especially if leaf-formation really took place as the defenders of such doctrines have represented: that is, if every successive leaf were produced as a *new* structure out of the old one (out of its base which becomes the internode), and if the whole stem were thus merely a concatenation of leaves shooting out of and growing above each other. But this is not so; the rudiment of the stem as an uninterrupted growth ("continuance") is formed *before* the leaves, while the latter, emerging as developments of the upper surface of the stem, are evidently members dependent upon and belonging to the axis, and forming with it one whole. Hence the structure of the internodes may be more aptly compared with the lateral structure of the animal body, and that of the leaves with its terminal structure. Thus we arrive at the shoot; and we must investigate the question, whether it should be considered as what corresponds best with the animal individual, or whether we must ascend still farther, up to the whole plant-stock.

The Shoot as the Vegetable Individual.

The first and most common view is that which considers the individual in plants, as in animals, to be merely each single specimen, i. e., each representative of the species which appears to be one whole from the connexion of its parts. To some extent this view is correct, for in a forest of trees of the same genus and species, in a meadow, or in a cornfield, each single tree, each stock of grass or of grain, appears as a single member of its species, as each single beast does in a flock of animals forming a

community. But the question arises whether these individual beings, regarded as such in this superficial way, can each be considered individuals in the same sense. When the flocks or societies of animals are numerous, as in an apiary, each hive or swarm will appear as an individual member of its species, and the more so in proportion to the closeness of the connexion between the members of such a community. Many flocks of animals whose members are organically connected during life, have until lately been considered to be individual animals; and even when the separation of the individuals is more complete, such conceptions are to a certain extent justified as long as the community is really a natural growth—when in fact it consists of members of one single stock—and we are not surprised to find that the oldest history of the human race describes the family itself, and the tribe which springs from it, as one person, named after its patriarch. As regards the plant-stock, even a superficial examination shows us peculiarities which will hardly allow us to consider it as an individual in the precise meaning of the term, and which calls upon us carefully to consider whether it is to be regarded as such an individual, or merely as an individual in the broader sense,—as one united family. Even our feelings aroused by the sight of the most ramified plant-stocks,—especially by a tree with its numerous branches, with the thousands of blossoms and fruits which it bears, and the numberless buds through which it will deck itself again in the following year with leaves and flowers—excite the presentiment that this is not one single being, one single life, comparable with the animal or the human individual, but rather a world of united individuals which have sprung from each other in a succession of generations, and although they do not separate, going through their particular cycles of existence,—here dying off, there reproduced, and thus building themselves up in uninterrupted succession into a family-tree, perennially laden with an increasing posterity. That such a view, so consistent with our healthy natural feelings, is corroborated by scientific investigation, I hope to show in the following observations.

Comparing plants with animal individuals, it is at once evident that the tree loses annually flowers and fruit,—the highest and noblest structures which vegetable life produces,—to generate them again in the following period of vegetation. Even the whole dress of the tree, even its foliage when compared with the trunk and branches, is only a superficial growth periodically dying off, and reproduced by the succeeding generation: in the paradoxical words of Schleiden:* "No tree has leaves."

* *Beitr.*, p. 152, where the following view of the arboraceous stem, as a common ground bearing many individuals is developed; but this whole view, after all, needs to be corrected by a precise limitation of its meaning by what follows it.

The leaves, in fact, never grow out of the woody portions of the tree, but only on its herbaceous extremities, which grow upon the woody stem as upon a ground formed by the process of vegation. This common ground, namely the woody stem, which is almost lifeless in comparison with the herbaceous parts engaged in active growth, is annually covered with a vigorous sheath under the protecting bark, and this sheath is the ground of the nourishment of all the vegetating herbaceous extremities. This sheath is the so-called *cambium*, a layer of active, living tissue which, contemporaneously with the lignification of the herbaceous extremities of the branches, becomes a new woody layer, united to the old trunk in the form of an annual ring—to be covered in its turn in the following period of vegetation with a new layer, which, again, will be the immediate supporter of the new generations. The history of the grand development of nature on the surface of our globe presents an analogy which may perhaps serve to set this relation in a clearer light. The successive geological formations superposed during the course of countless ages, present, buried in their depths, the traces of as many formations of the organic world, each of which carpeted the then superior stratum of the earth with a new life, until it found its own grave in the succeeding formation, when a new uprising of organic life took its place. In the same way the stem of a tree is a multistratified ground, in whose layers the history of earlier growths are legibly preserved. The number of the woody layers indicates the number of the generations which have perished, i. e., the age of the whole tree; a distinct annual ring is the monument of a vigorous season, an indistinct one of a bad season, a sickly one (which is often found among healthy ones) indicates the unhealthiness of the foliage of that particular year. The practised woodman can decipher many facts of the past in the layers of the trunk, e. g., a good season for foliage or for seed, damage by frost or by insects, etc.

Essentially the same relations as those seen in the tree, or the shrub, are to be found in the subterranean perennial growth of plantæ redivivæ (herbaceous perennials) whose subterranean stem (rhizoma), like the stem above the surface, emits annually a new generation of herbaceous growths; whose stalks however, unlike those of the tree, do not lignify and form a part of the common supporter, but die off wholly, or mostly, at the close of the season of vegetation.

The relations indicated above compel us to recognise a succession of generations in trees, shrubs, and perennial herbs; and thus our first idea of them as individuals is necessarily modified. Another remark may be made here which confirms our idea thus

modified. Natural *death* closes the life of the individual.* The development of the life of individuals in organic nature has a goal, an acme; after it has attained this goal its course draws to an end. This is not the case in the tree and the perennial herb. True the tree is destroyed by time; but this seems to result more from external, and in part mechanical causes, than from any internal decrepitude. The more numerous the generations which the tree builds up, one above the other, the greater is the distance of the growing extremities from the source of their nourishment; the thicker the supporting trunk the thinner is the layer of cambium which connects the new shoots with the extremities of the root by which the nourishment is absorbed. This increased difficulty of communication between the upper and lower extremities is probably the cause of the decrease of vigorous growth after the plant has arrived at a certain age. But in most cases external casualties are superinduced, which accelerate the termination of the tree's life. It is injured by wind and weather, the decay of the injured part spreads through the whole organism, various fungi fix themselves upon the tree, and are especially fatal when they attack the roots. Oftentimes the tree breaks down under the weight of the productions of its own vital powers, the luxuriance of its fruit. These statements are corroborated by the cases of trees of unusual age, now so well known through De Candolle's investigations. One of the examples adduced by him shows in particular that those trees whose branches have been prevented from breaking down by props or supports attain to a great age. I refer to the celebrated Linden in Neustadt on the Kocher, which, as early as 1229, was the cause of the town's being called "Neustadt an der grossen Linde" (Neustadt of the great Linden), whose wide-spreading branches were supported already in 1408 by sixty-seven stone pillars, and this number was afterwards increased up to more than one hundred.† The hoary tree still flourishes, having survived its many scientific admirers, among whom was my predecessor, to whom Botany is so greatly indebted, who visited and described it a few years ago, (in 1849).‡ Natural supports are more efficacious in preserving trees than even artifi-

* Cf. *Schleiden: Beitr.*, p. 151. "The idea of individual life necessarily implies as its distinguishing characteristic individual death, preconditioned in the organization itself." Although this remark is not universally true in many respects, yet I have adopted it for the light it is calculated to throw on the nature of the tree. For the very reason that natural death is the result of a determinate conclusion of the development, those shoots (vegetable individuals) which have no such conclusion frequently undergo no death at all except that of some of their parts: but this is a concomitant of animal life itself, (casting the skin, moulting, and the organic changes in the body). Cf. on this point Roeper: Linnaea, 1826, p. 439, and the following remarks on *Paris*, *Lysimachia nummularia*, *Adoxa*, etc., and the preceding ones on *Caulerpa*.

† *De Candolle: Physiol. Veg.* II, p. 988.

‡ *Link:* Erinnerungen an die grosse Linde bei Neustadt am Kocher (Flora, 1850, No. 8).

cial ones; since they not only prop the branches, but conduct nourishment to them by a shorter road, as is actually found to be the case in *Rhizophora Mangle*, in various species of figs, [Banyan, &c.], and other tropical trees, whose branches high in air send down strong roots into the earth. A similar example nearer home, though indeed on a much smaller scale, is found in the *Juniperus Sabina.* Its branches, which spring from a low stem, curve down to the earth, strike numerous roots, and raise themselves again, so that the comparatively feeble stem may carry a creeping crown of considerable extent, like a thick wood continually spreading, and which may continue to flourish in its parts, even when the communication between the original supporter and nourisher of the whole colony and the succeeding new growths, which are constantly receding from it, has finally ceased. A remarkable specimen of this tree stands in the Royal Botanical Garden at Schöneberg, which, if not as old as the Garden itself, which was laid out in 1679 under the great Elector, Frederic William, certainly dates as far back as Gleditsch's time, and his directorship commenced in 1744. The main stem is not more than 33 inches in circumference at eight inches above the ground, close under the place where the first branches originate; the centre-piece of the crown which belongs immediately to the stem, is only nine feet high, and has been dying off during several years, while the maximum diameter, from S. W. to N. E., of the hundred-rooted crown, which has spread out over the ground by the declination of the branches, measures 35 feet; the entire circumference of the crown, which amounts to about 100 feet, would be still more considerable if it had been permitted to spread on every side, and if the branches on the N. E. side had not been removed at an early day.

What has just been said of trees admits of no doubt as regards perennial herbs (plantæ redivivæ) with subterranean creeping stems or stolons. Such plant-stocks as those of the well-known *Paris*, *Anemone nemorosa*, *Convallaria majalis*, *Asperula odorata*, are undoubtedly exposed to none but a casual death.* All plants which renew the cycle of vegetative life repeatedly and without any determinate limits to their existence, and which I would hence call *anabiotic*, cannot therefore be considered *simple* individuals.†

* The same relations of great unlimited age are found in polyps which form stocks. Cf. Ehrenberg: *Abh. d. Acad.* for 1832, p. 382, 420, where among others, stocks of Mæandriæ and Faviæ are referred to, larger than a cord of wood—which may readily be supposed to have been seen by Pharaoh.

† I pass over the further question, intimately connected with this subject, whether the composite plant-stock itself, with all its subordinate generations, with all its possible divisions,—viz., the individual in the most comprehensive sense (in which Gallesio conceived it) has not a determinate term of life, though not easy to be ascertained, on account of the narrow space of time accessible to our direct experience.

At first sight the case seems to be different in the *haplobiotic** plants, which terminate their existence at the end of the simple process of development, with the formation of flowers and fruit; and this they do whether they exist one year, as *Adonis æstivalis* and *autumnalis*, *Nigella*, *Papaver Rhœas*, *Erigeron Canadensis*,† or for two years, as *Oenothera* and *Verbascum*, or for many years,‡ as *Agave* [Century-plant], the East Indian *Corypha*, and the Mexican *Fourcroya*,§ which suddenly puts forth its flowers only after 400 years of extremely slow growth, and ends its life with the formation of its first and long-deferred fruit. The development of these plants, when compared with that of the first mentioned anabiotic plants, seems at first to comprise only *one* generation, and to depend upon the development of *one* individual. But here, too, a closer examination shows conditions incompatible with the nature of the simple plant (the individual). One constituent element in the idea of an individual is, that the parts of the organism are *essentially* connected; yet the stock of annuals themselves presents a multitude of parts which bear no essential relation to the whole plant. This is true of a large part of the ramifications, of branches which may exist in one case and not in others, and

* De Candolle calls *anabiotic* growths *polycarpic* and *haplobiotic growths monocarpic*, terms which are useless from their ambiguity. With an equally inappropriate choice of terms he divides the first (Phys. Veg., II, p. 73) into *caulocarpic* and *rhizocarpic*, according as the stem which produces the fruit is permanent, or dies off down to the root; but the latter in fact never takes place in perennial growths; for in such cases the life of the plant-stock is preserved not by the mere root alone, but by a subterranean portion of the stem. It is one of the most remarkable confusions which a want of true biological ideas has engendered, that De Candolle should have regarded the simplest and most natural circumstance in the plant's life,—its death after having attained the goal of its development,—as an unnatural and to some extent casual occurrence, as a kind of sickness comparable to the succumbing of the mother in childbed, which he accounts for by the rapaciousness of the flowers and seeds. Röper, however, in a note to his translation of the above work, justly remarks that there are annuals with double flowers which die off to the ground although they produce no seeds. We may convince ourselves beyond a doubt that the flowers, on the contrary, are much less rapacious than the vegetative parts of the plant, that they even shut themselves off from the afflux of too copious nourishment; for many plants develop vegetative branches close under the terminal flower, as e. g., *Stellaria media*, *Datura*, *Mirabilis*, etc. In such cases the flower-stalk, which cuts itself off from almost all farther afflux of nourishment, remains slender, while the portions of the stem directly beneath, and the branches which spring from it, gorged with succulent matter, enlarge more and more, and attain a most disproportionate size.

† These plants, like other annuals which germinate in the autumn, are usually reckoned among biennials; but this is a mistake, for like our winter corn they are *plantæ annuæ hiemales*. So, too, many vernal plants, as *Teesdalia*, *Erophila*, *Cardamine hirsuta*, *Spergula Morisonii*, and many weeds of the winter corn, e. g., several species of tares, *Bromus secalinus* et aff.

‡ *Corypha umbraculifera*. Cf. *Rheede*, *Hort. Mal.*, iii, pl. 1–12. This is also the case in the palm-genera *Metroxylon* and *Eugeissona*, according to Martius (*Hist. Palm*, I, p. 108).

§ On *Fourcroya longæva*, cf. Zuccarini in the Nov. act. nat. cur., xvi, 2, p. 666 and pl. 48.

which are proved to be unessential by the plant's losing no essential function when deprived of them. For even when the plant does not produce them, it can fully consummate the object of its individual life; it can produce flowers and fruit. A glance at the examples just now adduced, *Nigella*, *Papaver Rhœas*, *Adonis*, etc., will make these statements obvious. The branches of these plants, each of which, like the stem, is crowned with flowers and fruit, are evidently only *unessential repetitions of the simple plant*, absolutely identical with the main stem, and hence to be ranked as equal to it in importance, i. e., equally to be viewed as particular individuals, and with as much reason as in Zöology we concede individuality to the branches of the coral-stock (polypidom), which are now universally acknowledged to be individuals, and which offer an analogy of decisive importance for ascertaining the nature of the branch in vegetables. In view of this analogy Ehrenberg regarded plants as aggregations of individuals.*

We can now turn back, and apply what has been shown to be the case in the annual herb to the shrub and the tree, each of whose annual generations now appears more distinctly than before to be, in their peculiar connexion, not one individual, but a world of individuals developing in the same period of vegetation and upon the same stem. To this intent many of the early botanists have expressed themselves, as I stated in the Introduction. Thus, B. Batsch, e. g., says of branches, that they shoot forth from the stem "as if they were so many plants rooted in it;"† and Goethe:‡ "lateral branches may be regarded as particular plantlets which are rooted upon the maternal stem, just as this stem is upon the earth." Among moderns, Unger, at the close of his investigations into dicotyledonous stems, says . . "Buds and the branches they develop are individual plants, which live by preying upon the maternal stem."§ Similar expressions are used by Schlei-

* *Abh. d. Akad.*, 1835, p. 247. . . . . "Hence a polyp-stock is a mass of animals. We have no satisfactory comprehensive expression for our idea of a plant. What an individual is remains still unknown; most of them are evidently aggregates of individuals which may be compared with coral-stocks." . . . The origin of coral-stocks is minutely described by Ehrenberg in the Abhandl. for 1832, where he makes the following remarks: "The coral structure is neither a mere structure composed of many animals arbitrarily conjoined, as Ellis supposed; nor one single animal with many heads, or with simple furcations, as Cavolini maintained; nor a vegetable stem with animal flowers, as Linnaeus expressed it; it is a body of families, a *living* tree of consanguinity, the single animals belonging to it, and continually developing upon the primary ancestor, are entirely isolated within themselves and capable of complete independence although unable to achieve it."

† *Bot. für Frauenzimmer*, p. 15–16.

‡ *Versuch d. Metam. d. Pfl. zu erklären*, p. 59. The words "just as" in the passage quoted imply too much, and remind us of Du Petit-Thouars' unfounded doctrine of the formation of the woody layers of the stem by the 'roots' of the buds which penetrate it.

§ *Ueber d. Bau u. Wachsthum des Dicotyledonenstammes*, p. 177. Here, too, "preying" is too strong a term.

den;* they are most definite in Röper's works.† Linnæus expressed the same thought in the words "*gemmæ totidem herbæ.*" And I am thus led to make a particular remark, which is intended at the same time to modify in some degree what I said before in relation to the annually renewed generations of trees. It is indeed true that branches of trees and perennial herbs, especially in temperate climates, first appear as buds; and in a more extended sense we call in general every young branch a bud, even if its parts are not, as they usually are, compactly arranged and folded together; still, all buds are not the rudiments of branches. *Lateral* buds are the only ones from which branches originate, and therefore they alone are to be regarded as new lines of development,—as individuals. Terminal buds, on the contrary, are nothing but still undeveloped parts of the (relative) principal axis: they are mere continuations and augmentations of the individual already existing, and are not to be regarded as commencements of a new one.‡ Hence, only those trees which produce no terminal buds, as the Linden, Willow and Elm develop new individuals and nothing else at each renewal of vegetation; while, on the contrary, those which do produce terminal buds also, as for example the Oak and Poplar, bear a mixed annual generation, which consists partly of new individuals, partly of old ones reawakening and continuing their development with renewed vigor.

I have already remarked how unessential the presence of branches is in many plants. A comparison of stocks grown on a rich soil with those of a poor one shows what license is given to plants in regard to producing branches, and how different the appearance of specimens of the same species thus becomes. Plants grown on a poor soil are often called dwarfs; but unjustly, for they present the most normal development of all essential parts, dispensing with everything that is unessential, and are much less

* *Grundz.*, ii, p. 4. "New identical individuals develop upon the maternal stem by continuing the growth," etc. Here the expression "continuing the growth," is improper, for the shoot does not "continue" the growth at all, but is a new growth from a new rudiment.

† "Omnis gemma solitaria aut ejusdem continuatio immediata et perpendicularis (caulis, ramus, ramulus, flos) individuum vegetabile vocatur." This is the most definite description I know of; for in this passage not only the branches so-called, but also every arbitrary shoot, even when it is merely a flower, is acknowledged to be a particular individual. Besides what I have stated in the text in regard to the appearance of terminal buds, I have only to remark, against the word "gemma," that in its growth every shoot does not enjoy a perceptible state of gemmation, i. e., a state of rest in which its parts are folded together. The term bud is applicable to but one state of a shoot or of its parts, and therefore cannot be a suitable expression for what is to be regarded as the vegetable individual.

‡ *Kutzing*, (*Phil. Bot.*, ii, p. 146,) aptly expresses these relations by calling the terminal bud the continuation of the "series of formations," lateral buds beginnings of a new "series of generations." In contradiction with these terms, however, he calls the bud an "organ" as long as it is connected with the natural individual—a term inapplicable to the bud as it is to the developed branch, of which it is the adolescent state.

inclined to malformations than the lusty giants of the rich soils. Not unfrequently we find diminutive speciments of *Erythræa pulchella s. ramosissima* which are branchless and perfectly simple, as they terminate with a flower after four or five pairs of leaves. More vigorous specimens produce two branches out of the axils of the highest pair of leaves, which after a single pair of leaves terminate in the same manner with a flower ; and branches of the second order may be also emitted from the axils of the two leaves preceding this flower ; and so on. In the first order of ramification the number of flowers amounts to three, in the second to seven, and so on ; in the seventh, which is not unfrequently attained, it amounts to 127 ! Here, if we would consider the stock or specimen as the individual, and the flower as the superior termination of the vegetable organism, comparable, say, to the head of the animal, this variation in the number of the flowers would be as astounding as if we were to learn that an animal might have 3, 7, 15, 31, 73, or 127 heads, according to circumstances. The same thing occurs in *Radiola linoides. Erigeron Canadensis*, which often grows to the height of a man and bears as many branches as a tree, presents dwarfed specimens scarcely two inches high and of a perfectly simple form.* After developing two early deciduous cotyledons it presents about 13 leaves on the stem, which are followed by a terminal capitulum of 21 involucral bracts and about 34 flowers. One middle-sized specimen about three feet high presented nearly 109 branches of the first order, out of which branches of the succeeding orders proceeded, together bearing about 2000 heads, and hence (reckoning the head at 34 flowers) 68000 flowers.†

I may here remark, that such unessential branches may be separated and reared independent of their parent stem : on which fact depends propagation by artificial divisions, which is so variously employed in horticulture. The most remarkable case of this artificial division is recorded by Miller : in the year 1766–67, he obtained 500 stocks of winter Rye, by dividing one stock and repeating the operation three times ; these 500 stocks emitted 21,109 spikes, bearing together 576,840 grains. Nature herself, as well as art, in various ways may effect such an independent separation of developed branches or of undeveloped buds, and this too either above or beneath the ground. Propagation of the Strawberry by its runners ; of the Potatoe and the *Helianthus tuberosus* by their tubers ; of bulbous plants by their bulbs ; of the

* Not counting the florets, which also are properly so many branches.

† Similar cases occur in most annuals. The forms of *Bromus mollis* and *racemosus* with simple spikelets instead of rich panicles, are well-known ; less known and less remarkable are the depauperate specimens of *Umbelliferæ* with one single unifloral umbel, some of which of *Scandix Pecten* are in my possession. I have also specimens of *Solanum nigrum*, one and a half inches high, with a solitary terminal flower.

Garlic by the bulblets formed in the process of flowering, and falling off like seeds; of the varieties of the beautiful *Achimenes* by the amentaceous or the strobiliaceous deciduous shootlets, are well-known examples of this process; and thousands of others might be adduced.*

The gardener can not only separate individuals, but unite them upon one stem. This is true not only of individuals of the same species, but even of those of different species; sometimes even of different genera of the same family. The Lilac is not unfrequently grafted upon the Privet (*Ligustrum*), the Pear upon the Mountain Ash (*Sorbus Aucuparia*), the Peach upon the Almond. By the insertion of a bud (inoculation), or of a developed sproulet (grafting), we are thus enabled to pluck different kinds of roses from the same bush, to gather different kinds of fruit from the same tree. It would evidently be a contradiction in this case to consider the whole tree, or the whole bush, as the individual; for we should then give the name to a compound of several species, or even of several genera.

In attempting to comprehend the vegetable individual in its simplest form, we have thus far spoken of unessential branches only, and have endeavored to show that they cannot be regarded as mere parts of the individual. But there is another kind of branches, those which are essentially requisite for the attainment of the end of vegetation,—for the formation of flowers and fruit. These occur in all plants which possess no terminal buds, and which must hence necessarily have some branches in order to attain the end of their existence. This is the case with the Evening-Primrose, Larkspur, *Orchideæ*, etc., whose lateral flowers are just such essential branches. If we demand that the individual should be a complete representative of the characters of the species, as is implied in the usual view, then we must add to the principal axis such branches as these,—without which the process of vegetation is not concluded, and on which, in fact, the most essential and characteristic parts of the plant make their appear-

* I will only adduce a few more of these examples, which might be multiplied indefinitely. Besides the Garlic (*Allium sativum*) in many other species of *Allium*, e.g., *A. oleraceum*, *carinatum*, *vineale*, *Lilium bulbiferum*, *tigrinum*, *humile*, and other species, *Gagea fistulosa*, *Ficaria ranunculoides*, *Dentaria bulbifera*, *Saxifraga bulbifera* and *cernua*, *Cicuta bulbifera*, *Polygonum viviparum*, *Begonia bulbifera*, *diversifolia* and other species, *Remusatia vivipara*, *Cystopteris bulbifera*—buds fall off above the ground (as bulblets). In *Stratiotes aloides* rosette-like developed axillary shoots separate close to the base. The separation of lateral shoots in *Lemna* is well-known; and it occurs in a similar manner in *Pistia*, by the separation of thin-stalked lateral rosettes, and in *Hydrocharis* in the separation of peculiar winter buds. When the inferior leaf-formation is gorged with sap, bulblet-like buds form from the axils of the root-leaves (frondes fundi) in *Saxifraga granulata* and many exotic species of *Oxalis*, in the same way as the bulb-brood of monocotyledonous bulbous plants. Inferior leaf buds which are placed on the ends of their stolons become free by the death of the runners in *Epilobium palustre*, *Lycopus Virginicus*, etc., and swell out and form little lumps. Cf. on this subject Wydler (Flora, 1853, p. 17—24).

ance,—and call these parts of the same individual. In this sense Schleiden's view of the simple plant might perhaps be justified, although, as he starts from different premises, he does not consider mere floral branches as particular individuals. He says: "If nothing but organs of reproduction, or flowers, spring from the bud we still call the plant a simple one."*

Here, however, we arrive at a contradiction, which shows us that we cannot carry out the idea of the vegetable individual with the requisite definiteness in this way, since we thus regard essentially similar branches, now as individuals in themselves, now as mere parts of individuals. As I have already remarked, Schleiden allows individual importance to branches which are identical† with the main axis; those on the contrary which produce flowers alone, and in this respect differ from the main axis, he regards as mere parts of the simple individual. This distinction when analyzed is perfectly nugatory; since it only lays down two extremes, between which there are an infinite number of gradations. Strictly speaking, there are no branches which are perfectly identical with the main stem, as is evident from the fact that no branch begins with cotyledons, as the main axis does.‡ Besides, the foliaceous leaves on the branch are almost always fewer than those on the main axis, and generally fewer in proportion as the point is higher where the branch originates. The arrangement of the leaves on the branches, also, often differs from the arrangement on the main axis, as e. g., in most of our broad-leaved trees, —in the Elm, Hazle, Chestnut, Linden, etc., in which the phyllotaxis on the main axis, and often at a later period in the so-called "water-shoots" (Wasserschossen), is spiral or decussate, while on the branches, it is, on the contrary, distichous. In *Alnus viridis* the phyllotaxis is tristichous on the main axis, and distichous on the branches. On the main axis of Cypresses and *Thuja* there are 3–4-leaved whorls; on the branches the pairs of leaves are nearly decussate; this is also the case in *Lysimachia vulgaris*. In the same way in *Equisetum* the number of the rameal verticillate leaves is always inferior to that of the cauline ones. While thus on the one hand the vegetative branches are nowhere entirely similar to the stem from which they spring, on the other hand it appears that those branchlets which seem to bear flowers only are usually more numerous than they seem to be; since in most cases one, two, or even more small leaves (bractlets), are present beneath the flower, which may easily escape notice on account of their diminutive size, although their existence may

* *Grundz.*, ii, p. 4. † *Grundz.*, ii, p. 4.

‡ The basillary cotyledons of the branches, indeed, have been compared to cotyledons. This comparison is partly justified in view of the commencement of phyllotaxis on the branch; which often resembles that on the main axis, whilein regard to form and consistency almost all resemblance disappears.

be often ascertained with certainty even in those cases in which they are not visible when the flower has reached its complete development.* If we are to deny individuality to those buds (branches) only which are composed of a flower alone, as a strict interpretation of Schleiden's language demands, we should have to draw a most unnatural and often impracticable line of demarcation between branches which, physiologically speaking, are perfectly homologous (floral branchlets which really have no bracts), and those which bear imperceptible or even suppressed (abortive) bracts. If on the other hand we would reckon the latter also among the branches which are not individuals, then it may be contended that there is such a series of gradations in regard to number and vigor in the leaves which precede the rameal flower, that it is impossible to draw a dividing line even in this manner.

The above-mentioned distinction between unessential and essential branches seems to afford a better stopping-place, no matter

* In fact, all the constant lateral flowers of *Primulaceæ*, *Crucifera*, *Capparideæ*, *Resedaceæ*, *Balsamineæ*, *Orchideæ*, never have any bractlets. Among monocotyledonous plants in many cases there is only one bractlet; among the dicotyledonous there are generally two. *Gesneriaceæ* have generally three; *Empetrum* and *Santalum* have four, *Eriostemon* five, *Polemoniaceæ*, *Cuscuteæ* and other plants with panicled inflorescence an indeterminate number. We possess the following means of showing the existence of suppressed bractlets: 1. The position of the parts of the flower relatively to the axis of origination from which the lateral flowers spring. 2. Analogy. 3. The study of malformations. 4. Observations of the flower's development. The first criterion can be applied only where we can determine the succession of the parts of the flower. The position of the parts of a lateral flower depends in fact upon determinate laws of rameal origination; when they do not harmonize with these laws we must conclude that preceding leaves have been suppressed. In this way, e. g., we can explain the very common position in the 2–5th arrangement of the calyx with the second sepal posterior, by supposing two bractlets according to the fixed law, while it cannot be explained without these bractlets. Analogy aids us most by confirming our conclusions, as e. g., in the families *Scrophularineæ*, *Labiatæ*, etc., in which many genera present distinct bractlets, while others appear to be without them. In monstrous flowers (in cases of *antholysis* and *chlorysis*), sometimes without any other malformation, bractlets otherwise imperceptible appear in an abnormal growth. Not unfrequently in *Digitalis purpurea*, which in its normal state presents no bractlets, but in which we inferred their original existence from æstivation and the position of the calyx relatively to the axis, I have found bractlets developed in the most heterogeneous degrees, especially on the lowest flowers of the raceme of cultivated specimens. C. Schimper and myself have both observed the same fact in *Tropæolum majus*, which, like most species of this genus, presents no trace of bractlets in the normal state. We have seen them in the form of very small, white, subulate leaves about in the middle of the flower-stalk, while the flower remained unchanged in all other respects. Their existence, however, was already indicated by the position of the quincuncial calyx relatively to the axis, as well as confirmed by analogy, for *Tropæolum ciliatum* R. et. P. (Pöpp. et Endl. Nov. Gen. t. 38) in its normal development has two round and prettily ciliated bractlets on the the flower-stalk. I have mentioned the history of development last, not to disparage study, but because the morphology must be rightly understood beforehand by means of comparisons of developed structures, and because in its present stage the development is incapable of giving us reliable information in regard to all the leaves which are present in the germ, though they may not develop. To know what parts then exist we should have to be able to distinguish the leaf as a cell or a group of cells before it rises to view above the surface of the stem.

whether the branch bears nothing but a flower or not. We might say, all essential branches must be regarded as individuals since they repeat the process of specific development laterally, and can become independent plants, as layers, whether natural or artificial. Those branches, on the contrary, which appear as necessary members in the line of development which is advancing towards flower and fruit, and which therefore complete the series of formations belonging to the species, and without which the plant is either unable to eke out its vegetable life or to accomplish propagation, must be regarded as members of one and the same history of development. Let us take a case where the main stem bears only proper leaves, branches of the first order only bracts, and those of the second order only flowers and fruit, as is really the case in *Plantago*, *Melilotus*, *Veronica officinalis* and *Chamædrys*; here it is evident that these three divisions cannot be isolated; that all three must necessarily be present in order that the specific life may attain a complete representation in one individual.*

Notwithstanding the importance of this discrimination between essential and unessential branches, it cannot, when analyzed, establish a distinction which will enable us to decide upon their importance as individuals; for even those branches which appear unessential, in relation to the formation of flowers and fruit, may yet be essential to the plant in other relations: as when they appear as characteristic elements of the vegetable structure, or when they play any important part in the economy of the plant, as I have shown *in extenso* elsewhere.† Nay, more; one and the same branch, as to whose nature there seems to be no doubt, may appear either as essential or as unessential, according to circumstances. When those branches which conduct the structure to a higher stage of its development appear in great numbers on a principal axis, as e. g., in indefinite racemose or spicate inflorescence, the lateral branchlets appearing as flowers are then indeed, generally speaking, necessary to the plant's full completion of the series of formations, and in this sense essential; but their number is immaterial as regards this completion; and this the plant itself shows in producing either a larger or a smaller number of them; sometimes the number is reduced to one.‡ Therefore, properly speaking, only *one* lateral flower is essential: and we may arbitrarily consider any one of the number to be this essential one. Hence each of them may be regarded indifferently as essential or unessential. This is not the case in those racemes and spikes which possess a terminal flower, as is the case in many

* [But why assume (as here and *supra*) that the species must attain a complete representation in a single individual in vegetables?—since this is by no means the case in the higher (unisexual) animals, where there is no doubt as to what corporeally constitutes the individual,—that is, in the very cases whence we derive our idea of individuality, and the standard of comparison which our author is endeavoring to apply to the case of plants. A. G.]

† v. Verjüngung, p. 41, et. seq.

‡ E. g. not unfrequently in the raceme of *Lathyrus odoratus*.

Campanulaceæ, e. g. in *Campanula rapunculoides.* Here all the lateral flowers are unessential: yet if the terminal flower is cut off, the lateral branchlets which bear the flowers at once become essential. Such a change is not always artificial, for it often happens naturally, as there are plants in which the terminal flower may be either present or absent. *Agrimonia Eupatoria*, and *Campanula rapunculoides*, are examples of this variability.*

We can cut this Gordian knot only by deciding to consider every branch as an individual, however appearances may be against it, provided that we have other grounds sufficient to regard branches as individuals. The genesis of branches justifies us in so doing; for each branch is not a direct continuation laterally, is not a development belonging to the stem (like the leaf), but is a new formation; like the main axis itself, it has its own centre of formation, with its peculiar development. Branch and stem, main axis and lateral axis, differ therefore only in their origin and relative position; but they are essentially of the same nature; they are united in the idea of the *shoot.* The stem is the primary and principal shoot of the whole plant, the branch is a lateral shoot in reference to the main shoot; but it can itself become a relatively main shoot, and the stem of a succeeding generation of shoots in its turn. As far, then, as we are justified in speaking of vegetable individuality at all, we must hold fast to the individuality of the shoot: *the shoot is the morphological vegetable individual;* is that form or that part of its specific realization which is analogous to the animal individual, if any part is.

In zöology we give the name of individual to every whole which is controlled and bound together from one vital centre. Since such an internal domination of the organism as that which characterises animal life is wanting in plants, whose existence is a process of growth directed externally alone, we can only demand, as the criterion of vegetable individuality, that the individual shall be formed in direct continued development from one centre, and thus in accordance with its origin, *shall, in all its parts, belong to one centre.* Now this is the character of the shoot. Its centre of formation has been known since C. F. Wolff's celebrated "Theoria Generationis" (1759) under the name of "*punctum vegetationis*;" it is about what is called in

* *Agrimonia Eupatoria* bears usually one spike without any terminal flower; in weak specimens, a terminal flower not unfrequently makes its appearance which opens before the upper lateral flowers. This has been observed by Wydler (Bot. Zeit. 1844, p. 642). In *Campanula rapunculoides* the case is just the contrary: its looser spikes are usually terminated with a flower, while denser ones end in a coma of bracteal leaves, without any terminal flower. *Dictamnus* resembles *Agrimonia;* while *Triglochin* (especially *Tr. maritimum*) on the other hand imitates *Campanula.* Even in plants in which the essentiality of the lateral position of the flower is expressed by their zygomorphic development, terminal flowers make their appearance in some cases; they then resemble *Peloriæ.* This is the case in *Linaria*, *Orobanche*, and a *Digitalis purpurea monstrosa* (described by Vrolik, Flora, 1844, No. 1), which propagates by seeds, and is now widely disseminated in our gardens.

common life the "heart," of the plant, or, at the first appearance of the lateral shoot, the "eye." The whole future of the plant slumbers unseen within it; leaf after leaf arises out of it, step by step, at a measured pace, prescribed by law, until (in case the shoot is destined to conduct the development thus far) the series concludes with the last formation, that of the carpels, which close over the dying point of vegetation and form the fruit. In this progress the centre, always keeping the lead, is ever advancing, rising more and more, and leaving behind it an axis arrayed with the organs already formed. Hence we may designate the vegetable individual as *the sum of the parts belonging to one axis.* Just as the body of the animal has only one trunk and one head, the shoot has but one axis and one apex. As the trunk of the animal has a second extremity opposite to the terminating head, and gradually dwindling down till it forms the tail, so the perfect shoot has a second extremity opposite to that which terminates with the most perfect structure (the fruit), and dwindling down to an indeterminate end, the root, by means of a *punctum vegetationis* turned downward.*

But it will be objected: is not the vegetable shoot indefinitely divisible, can we not cut it up into an arbitrary number of pieces, each of which is capable of reproducing the whole plant in its turn? Were this the case the phenomenon would not be without its parallel among the lower animals. But this is not the case. The supposed divisibility of the vegetable shoot, at least in perfect plants (the Phanerogamia) to which I am now alluding, is a delusion, which rests simply upon the fact that the formation of new shoots has been confounded with a reproduction of the shoot as such. As the injured shoot has the faculty of producing new shoots, so the parts of the divided shoot have also this faculty in many cases; but this is no re-completion of the shoot itself; the fragment of the old shoot can continue to develop in one single case only: when, in fact, it bears the apex of the axis with the point of vegetation. Let us examine this case more closely. If a shoot is divided transversely, under certain circumstances the upper part, on which the *punctum vegetationis* ("the heart") is

* Aristotle, on the contrary, considered that the root, being the imbibing organ, was the part of the plant which corresponds to the upper part, to the head and mouth of the animal; and he regarded the stem as the inferior part. He found the cause of this topsy-turvy position of plants in the necessity under which they labor of drawing their nourishment from the earth, as they are incapable of moving from place to place. In this respect he compares plants to muscles ((ὀστρακόδερμα), which also have their heads turned downwards. Cf. *Wimmer: Phyt. Aris. Frag.* 56–65. This comparison of the root with the animal's head is however, morphologically speaking, inverted; for as the highest stratum of the spinal chord (the sensorial portion) attains its maximum state of development in the head of animals, it can only be compared to that extremity of the plant's axis in which the highest and noblest part of the plant is exhibited. Besides, the peculiar and striking characteristic of the animal's head, its involved structure terminating the organism, is by no means to be found in the root end of the plant; but it is seen in the opposite end which terminates with flower and fruit.

still remaining, may continue the development; but the lower part is nothing but a stump, aud continues to be a stump which can never complete itself by a terminal shoot, and which never fails to die if it is not nourished by lateral sprouts formed before, or sometimes after, the division took place, and thus kept alive by its posterity. This cannot be called divisibility, in the usual meaning of the term; the whole phenomenon, on the contrary, strongly reminds us of the capacity animals possess of losing the less essential caudal extremity without any cessation of life. In favor of this view the fact may be adduced that a similar phenomenon occurs in the normal process of development of plants and animals. As there are animals which may spontaneously lose the posterior extremity of their body during the course of their development, as e. g., *Cercaria*, *Comatula*, frogs, etc., so there are also numerous plants in which the posterior extremity gradually dies off, and is cast aside, during the course of growth, while the anterior end of the shoot, which bears the *punctum vegetationis* continues to unfold; as is seen in the growth of many mosses, especially of Peat-mosses, in the creeping and climbing rootstocks of Ferns and *Aroideæ*, in the long creeping stems of *Lysimachia nummularia*, the little subterranean creeping rootstocks of *Paris*, in most plants which possess a *radix præmorsa*, as e. g., *Succisa pratensis*, the perennial species of *Plantago*, in *Tormentilla*, etc., with which the perennial bulbs of monocotyledonous plants agree in all essential respects; and finally, this is especially remarkable in *Utricularia*, and in *Selaginella increscentifolia*, whose apices only form close buds, and last through the winter, while all the remaining parts of the shoots perish. If the shoot is indivisible transversely, it is still less so longitudinally. There is not a single case to prove that a shoot longitudinally divided can as such continue to develop; nor do we know of a single case where such a longitudinal division takes place spontaneously. What has been usually described as a bifurcation of the stalk depends in the Phanerogamia in every case upon a true ramification which takes its rise laterally close under the apex, as I have already described it in the case of *Erythræa pulchella*. As a *normal* formation no immediate division of the stalk occurs among Phanerogamia; for the phenomenon known as "fasciation," which might be adduced here, is always a monstrosity.* The stalk, or axis of the shoot, is hence indivisible in

* Fasciation depends upon a real division of the punctum vegetationis into two parts of equal importance; in the simplest case it produces a simple division into two parts. Here neither of the two parts can be regarded as a branch of the other. If repeated bifurcations follow each other in the same plane, and in unbroken connexion the well known "ribbon and fan" like forms arise which however usually end at last in single apices. Very rarely more than two parts lying in different planes are produced by the division of the *punctum vegetationis*, a case which I have noticed in the capitula of Compositæ. The rarest phenomenon which bears upon our subject is the annular fasciation, in which an annular border arises from the simple point of vegetation, of which I shall speak more at large in the following Part, when

the higher plants, in the same sense that the body of the higher animals is indivisible.* The only phenomenon which might be described as a division of the stalk is leaf-formation. This, however, is not a division into new stalks, but a formation of subordinate parts belonging essentially to the stalk, as it were an eradiation of the stalk itself, which may be aptly compared to the formation of the extremities in the animal body. We may therefore justly describe the shoot, or the vegetable individual, as an indivisible axis,—as an axis with its appertinent radii which are inseparable from, and regularly arranged by, its own development. With the first appearance of the branch a new axis is formed, and a new system of subordinate radii appears. However completely the branch may contrive to interweave itself with the trunk during the course of its development, it always owes its origin to an accessory point of vegetation which develops into a particular axis. The vegetable individual thus presents in its nature a certain analogy to the mineral individual,—the crystal,—as well as to the animal individual; for the crystal is determined by the relation of its parts to one and the same system of axes. As soon as this system of axes holds another position there results another individual, which may be distinguished even when two or more individual crystals intersect, so as to form twin crystals, or stellate crystals.

In the preceding considerations on the indivisibility of the axis I described the leaves as its radiations,—as members of the stalk, and belonging essentially to it,—and I attempted to distinguish the leaves from the branches, by considering the latter as new axes. But how are leaves and branches distinguished in their genesis? Are not the branches as much radiations or lateral members of the stalk as the leaves? It would lead me too far from my subject to make a fundamental critical investigation into this question, and to examine the existing views of the mode of formation of leaves and branches, especially as investigations into this subject have not been complete enough to enable us to obtain reliable results. I can therefore only allow myself a few hints in this place. The leaf originates in the earliest period of the formation of the stalk; and its rudiment is contemporaneous with the first stages of the formation of tissue in the *punctum*

I compare the relations of growth in the Cryptogamia. A division of the individual corresponding to fasciation in phanerogams and to diethotomy, its homologue, in many cryptogams also occurs in the animal kingdom, as appears especially in many genera of corals, e.g. *Caryophyllaa* whose stocks are formed in this manner exclusively, and in *Astraa* and *Favia* in which it appears in conjunction with shoot-formation (gemmation), as was shown by Ehrenberg, (Beiträge, etc., Abh. der Acad., 1832, p. 242). Ehrenberg explains the form of *Dadalina* as a result of incomplete termination of the individuals in gemmation; in appearance it resembles the coxcomb-like forms of fasciation as they occur in a remarkable way in some monstrous *Cacti* of the genera *Mammillaria* and *Echinocactus*, as well as in *Celosia cristata*, well-known as an ornamental plant.

* [Some criticisms upon this may be given at the close of the whole memoir. A. G.]

vegetationis. A leaf can never be formed at a later period from the developed axis. It is a necessary consequence of the manner in which the leaf originates, that an absolute dividing line cannot be drawn between leaf and axis; for the subsequent position of the leaves upon the organism affords no standard of appreciation, especially as most of them do not mark the basis of the leaf, which loses itself in the axis. Earlier, before the extension of the axis begins, the rudiments of the leaves are always closely pressed together, so that they appear as a peripherical development of the axis itself, occupying the whole upper surface, and dividing it into clearly defined planes, which may be recognised even in the developed state, in those plants whose foliaceous *pulvini* are distinctly marked, as e. g. in many Ferns, most acerose plants, in Cacti, and particularly in *Nymphæa* and *Victoria* where the *pulvini* may be distinguished even in the interior of the axis. The primitive vascular system of the axis enters directly into the leaves, and ramifies there; while the woody layers of the stem, which are found later, have no connexion with the leaves. With branches the case is totally different. In their origin and development they always succeed the leaves; and even at a much later period, when the leaves have been long cast off, shoots may originate in places where, at an earlier period, no trace of a rameal rudiment, or of an eye, was to be found. If we now consider the axillary shoots,—i. e. those branches whose position is predetermined by the situation of the leaves,—at an early period we shall find their rudiments, even though they develop very late or not at all, in the form of a circular and slightly prominent gibbosity, which may be compared with the apex of the axis; or rather, it is an accessory *punctum vegetationis* forming near the apex. The circumstance of the epidermis of the axillary shoot's being a continuation of that of the stem, is explained by the early date at which it originates; for this takes place at a time when the surface of the axis has not yet lost its flexibility. The eye is shown to be an independent centre of vegetation by its subsequent internal and external conformation; for it not only develops leaves upon its surface, and this too with an independent commencement of its phyllotaxis, but even in its interior the first system of vascular fibres seems to be formed independently of that of the main axis; as originally it lies upon it, and afterwards becomes intimately blended with it by later layers of tissue. Notwithstanding the intimacy with which later formations of woody tissue unite branch and stem, still, according to Unger's investigations, no immediate influence is exerted by the branch upon the conformation of the stem, since the stem owes none of its essential parts to the branches.* This independence of the branches is shown still more decisively in adventitious shoots, whose posi-

* *Unger: Ueber den Bau des Dicotyledonen-Stammes* (1840), p. 65, *et* 66.

tion is not predetermined by the leaves. Originating at a later period, they take their rise not from the surface but from the cambium layer,—the internal tissue which preserves the faculty of producing new growths. Hence if they would come to the light of day they must break through the bark. Their origin has been particularly described by Trécul.* W. Hofmeister, however, as I have already remarked, succeeded in tracing it in *Equisetum* back to the first cell, a cell in the interior of the stem. As is the case with axillary buds, such adventitious buds sometimes remain undeveloped for a long time (ten years and more) without losing their vital activity; a fact to which attention has lately been called by C. Schimper,† in a report on exostoses. When this is the case they not unfrequently develop into spherical or conical wood-kernels, which continue to exist without any connexion with the ligneous body of the maternal stem; this is especially the case in Beeches and Poplars.

The individual nature of the shoot is confirmed not only by the mode, but by the place, of its origin. While the organs of the individual organism,—the leaves of the plant,—occupy a position determined with geometrical accuracy, shoots on the contrary can arise out of almost any part of the plant, wherever indeed any cambium exists; and they may be even enticed by art out of places where they do not usually appear. There are shoots from the *stem*, the *root* and the *leaves*. In herbaceous stems they appear in situations determined by the leaves (in the axils of the leaves), while they may be found anywhere on old woody stems‡ as adventitious buds, or on any part of the lignified roots of most dicotyledonous woody growths, and even on some monocotyledonous ones, as in *umbraculiferæ*.§ Shoots appear less frequently on the roots of herbaceous plants.‖ Shoot-formation from leaves has often been discussed and described in regard to many plants, especially *Bryophyllum*, *Cardamine pratensis*, *Drosera*, *Malaxis paludosa*, etc. A fine example of this is shown by a *Chelidonium majus var. laciniatum* reared by Bernhardi in the Botanical Garden at Erfurt, from whose leaves

* *Trécul: Recherches sur l'orig. des bourg. adv.* Ann. des sc. nat., viii, (1847) p. 268.

† In Sept., 1852, in the Versammlung der Naturforscher in Wiesbaden.

‡ Rarely scattered shoots appear on the herbaceous stem, and especially on the first internode under the cotyledons, as Röper (Enum. Euphorb. 1824) first showed in *Euphorbia*, and Bernhardi in the germ of *Linaria*. A specimen of *Begonia manicata*, *dipetala* cultivated in our [Berlin] Botanical Garden, which is probably the same species as the *B. phyllomaniaca* of Martius, presents the case of a plant which produces a multitude of shootlets in the whole leaf-region; they arise from the sappy stem which is not yet hardened, soon after the fall of the leaves.

§ According to Rheede, *Corypha umbraculifera* sends forth root-shoots when the stem dies off after the fruit has ripened.

‖ I have often observed them in *Linaria vulgaris*, *Helichrysum arenarium*, *Rumex Acetosella*, *Ajuga Genevensis*, *Jurinea Pollichii*, *Nasturtium sylvestre* et *Pyrenaicum*. According to Wydler, they often appear in *Viola sylvatica*.

floral bractlets arose, partly unifloral, partly multifloral, without any preceding leaves.* Shoots may be allured by the gardener out of most leaves which do not wither too soon.† Finally, the little budlets in whose bosom the germ of the new plant is formed and developed, and which we call seeds, are a kind of shoots, which in most cases owe their origin to leaves, (carpels) out of which they spring (on the margins, which unite to form the placenta) or more rarely, out of their whole inner surface.

While thus, on the one hand, all the facts seem to unite in establishing the individual nature of the shoot, on comparing shoots in their qualitative relations, phenomena are brought to view which seem to contradict such a view of its individuality. The higher departments of the animal kingdom usually present as individuals representatives of the specific type agreeing in all essential respects, though, perhaps, not perfectly identical. The fact of the separation of the sexes was all that modified this view; and here, indeed, the essence of the species does seem to be divided between two different individuals. Attempts have not been wanting to obviate this contradiction by the Platonic doctrine of the original unity of the sexes, by the assertion of Paracelsus;‡ that, in fact, the two together must be regarded as the one real individual,—and such like.

This contradiction to the usual view of what constitutes the individual is shown in a far higher degree by *qualitative* comparisons of vegetable shoots, not merely of the same species, but also of the same stock. Thus we see, e. g., in *Equisetum arvense* (Field-Horsetail) shoots totally different in aspect proceeding from the same root-stock; in early spring they are pale, discolored, unbranched, terminating with a strobilaceous-like fructification; later, green and foliaceous ones appear, verticillately ramified. Investigations into subterranean vegetation show even other varieties of shoot-formation, viz., offsets dwindling down to a point, and club-shaped buds which, at a later period, drop off of themselves. The Colt's-foot (*Tussilago Farfara*) presents similar phenomena, in early spring putting forth leafless shoots, with asparagus-like scales terminating with yellow capitula, which in summer are followed by others bearing leaves. The flowers in the little capitula of the first present a third variety of shoots in their lateral branchlets. Even in common life we distinguish

* I may add to the examples I have given of shoot-formation taking place out of the leaves, one which I observed in June, 1853, in *Levisticum officinale.* I found, in fact, in several species of this Umbellifera, one or more, frequently two, shoots in the points of division of the leaves, which, after producing a few weak leaves bore a small umbel. (Later note.)

† *Kirschleger* (Flora 1841, No. 2) notices a fine example of this in *Gloxinia speciosa.*

‡ "For this ye must know: man without woman is not a whole; only with woman is he a whole. That is as much as to say: both together make man, and neither alone."

leaf-buds from flower-buds, on many trees. Let us consider this relation in the Cherry tree, for example. On the same branch we find, on the one hand, buds which develop into branches bearing leaves, without producing flowers; on the other hand some bearing only little squamate leaves on the shortened axis, from whose axils the flowers rise and form a third kind of shoot.

On examining closer into the real origin of these differences, we find their ground to be a partition of the different steps of the metamorphosis (of the formations) among different shoots. True there are many plants which go through the whole series of formations, from the inferior* and the foliaceous formations up to flower and fruit; but the cases are quite numerous in which this does not take place, in which the single shoot is not able to produce all the formations. Thus there are shoots which are only able to realize the lower steps, and never attain to flowers and fruit; while others overleap all the inferior degrees and commence immediately with the formation of flowers. Hence, on the one hand, we see the metamorphosis interrupted, a stoppage taking place at a determinate step; on the other, the metamorphosis attained by passing over the intermediate steps. Still more remarkable are the cases in which the retardation is not merely an interruption at a determinate step, but appears as a real retrogression in the metamorphosis, whereby an alternate rise and fall,—an oscillation,—usually takes place, which may at last pass over in victorious progress to the formation of flower and fruit; though in most instances it prevents the shoot in question from ever attaining its end. *Helleborus niger* is an example of the first case; for after many years of inferior- and foliaceous-leaf formation, at last it attains superior leaves and fruit by overleaping the formation of foliaceous-leaves which until then had prevented its farther progress.† Many of our trees with true foliage present examples of the second case. Their branches commence with bud-scales (inferior-leaves), the succeeding foliaceous branch ends with a terminal bud, (thus falling back to inferior-leaf formation,) and in the next period of vegetation they rise

* On the terminology of the leaf-formations, see *Wydler:* Bot. Zeit., 1844, 36tes. Stück., and A. Braun Verjüngung, p. 66. (Henfrey's Transl. Ray Soc., 1853, p 62, T.)

† Analogous cases occur in the branches in *Æsculus* and many Maples which attain to flowers. Among herbaceous plants *Anemone nemorosa* and *Asarum Europæum* also belong here, and especially remarkable is the Tulip, the plants of which, not yet ripe for flowering, annually develop one single foliaceous leaf, followed by a central-bud hidden in the middle of the bulb and composed of several inferior-leaves. This bud preserves this position in bulbs deep in the ground, but in those nearer the surface it is, as it were, led out of the centre of the bulb, and sinks deeper into the earth, causing an indentation of the surrounding base of the preceding leaf in form like a spur, boring through the old bulb and penetrating vertically into the ground, and at the same time sinking itself into a deeper stratum with the spur;—an arrangement explained, but not with sufficient clearness by *Henry* in Nov. Act. Nat. Cur., vol. xxi, p. 275, t. 16 et 17.

again to foliaceous-leaf formation,*—as in the Oak, Beech, and Poplar. A similar oscillation between inferior-leaf formation and foliaceous-leaf formation, keeping pace with the change of season, is seen in the creeping main-shoot of *Adoxa*, and in the stock of *Hepatica nobilis*, creeping close to the soil, with its short internodes, and which in so far deserves its French name (la fille avant la mère) as its flowers, which unfold before the foliage, do not belong to the same individual as the foliage, but are produced laterally as a "daughter generation" from the axils of the inferior-leaves of the maternal stem.† A similar phenomenon only in a higher degree, (a rising and falling between foliaceous- and superior-leaf formation,) is presented by those plants whose inflorescence ends in a foliaceous coma, as is remarkably the case in the Pine-Apple, and also in the New Holland species of *Melaleuca* and *Callistemon*, whose crowded, brush-like inflorescence (i. e. the region covered with superior-leaves and bearing the flowers in the axils of these) returns and forms foliaceous-leaves, and in the following year again attains an inflorescence.

While every leaf-formation may bring the progress of the metamorphosis on a single shoot to a consummation, it is conceivable that one shoot may be allowed to each step for itself alone. Thus, there are shoots which represent inferior-leaf formation alone; e. g. the root-stock of *Paris quadrifolia*, the tuberiferous branches of the rhizoma of the Potatoe,‡ and there are some which are endowed with the foliaceous-leaf formation only, as the primary axis of many species of *Veronica*, the sterile leafy branches of several *Euphorbiæ*, as well as the leafy branches of those woody growths which have no bud-scales and no terminal inflorescence, (e. g. *Rhamnus Frangula*). Cases of pure superior-leaved shoots may be seen in the peduncles of *Veronica Chamædrys*, *officina-*

* In such librations, of course, the formation of the flower can only be attained by particular branches, deviating in character from the rest,—the catkins which pass over leaf-formation advancing from the inferior-leaves immediately to the superior-leaves out of whose axils the flowers are emitted.

† The same obtains in *Galanthus nivalis*, in which every annual generation consists of one inferior-leaf, one foliaceous-leaf with a vagina, and one without a vagina, which follow each other in simple alternation, in a distichous arrangement. The flower, as a branch, is emitted from the axil of the second foliaceous-leaf while the direct continuation of the shoot returns again to inferior-leaf formation. In striking contrast to the extremely simple relations of this plant we find *Oxalis tetraphylla* and other species of that genus, in which the subterraneous main-stem also presents an alternation of inferior leaf-formation and foliaceous-leaf formation, advancing with the change of season, but conjoined with a rare abundance of leaves and a complicated phyllotaxis. The number of the inferior-leaves amounts to several hundreds; and transverse sections of the bulbs, which last through the winter and are formed by the close approximation of these leaves, form some of the prettiest specimens of phyllotaxis, showing 21-15 arrangement through easily computable 8-, 13- and 21-ranked oblique spirals. The number of the foliaceous-leaves is not so large; they develop in the summer, and form an 8 to 13 leaved rosette, out of which the axillary inflorescences issue, with their long peduncles.

‡ In case (as sometimes occurs) the tuber does not pass through this formation and advance to foliaceous-leaf formation. The tuber is the thickened apex of the inferior-leaf shoot. Cf. the figure by *Turpin:* Mém. du Mus. d'Hist. Nat., t. 19, pl. 2.

lis, etc., in the (always lateral) spike-bearing scapes of *Plantago*, and the racemes of *Convallaria majalis*, which shoot out of the axil of the highest lower-leaf as branches. Even the leaf-formation belonging to the flower can be divided among different shoots, and thus the flowers may be produced piecemeal, so to say; as is the case in all diœcious plants, where the two most essential formations of the flower (the stamens and pistils) are found, not in the same flower, but in two separate ones. Even the less essential parts of the flower, the sepals and the petals, may occur separated from the other particular shootlets; as may be seen in the neutral flowers in the coma of the spike of *Muscari comosum* and in the ray-flowers of the cyme of *Viburnum Opulus*. The destitution of the shoot may be carried so far as to cause it to produce but one single leaf, or one single formation (whether from the sphere of the plant-stock, or from that of the leaves); in which case the individual represents only one single organ; as, for instance, in the branches which form the axis of the inflorescence in *Vicia monanthos* and other Leguminosæ with racemes reduced to one flower, bearing one single superior-leaf, from whose axil the flower proceeds. The male flower of *Euphorbia* is a peduncle whose flower consists of one single stamen.* Must we, now, still regard as individuals, these shoots, so partially endowed, and the last-named so destitute? Certainly! For if the individual can fall short, though ever so little, of the perfect realization of the specific idea, then there are no limits to its imperfection and destitution; for, after all, the realization of this vegeta-

* The genuine cases will be of rare occurrence if we look at the cases which belong here rigorously, that is, if we take into account the dwarfed foliaceous formations which may possibly exist, suppressed or scarcely discernible. The male flower of *Euphorbia* itself properly belongs here only in appearance, as two small scales (inferior-leaves) occur, more or less developed, at the base of the peduncle. The small involucre of the male flower proceeds to develop itself out of one of these scales. (Cf. *Wydler:* Linnaea, 1843, p. 409.) Another example of a one-leaved shoot (though a spurious one) is presented in the Californian *Pinus monophyllos* (*Fremont*), whose lateral branchlets bear a fascicle of needle-shaped leaves reduced to one single needle: but this, as well as the pair of such leaves of our ordinary pines, is preceded by a vagina composed of several bud-scales. Perhaps another deception is played upon us in this case, for the perfectly round form of this needle excites the suspicion that it may be composed of two which have grown together through their whole length. The seed-bearing fruit-scales of the cone of *Abietinæ*, which are placed in the axils of the scales, also appear to be one-leaved shoots; but the series of changes which these scales present in cones of *Pinus Larix* which have completed their growth, proves that these fruit-scales are composed of two concrete leaves. The spurious axis of the Grape is a concatenation of alternating one- and two-leaved leaf-shoots, if we do not count the one or two little dwarfed superior-leaves, which in most cases are perceptible on the apex of the single shoot which finally forms a cirrhus. *Ophioglossum* presents a genuine case of a one-leaved shoot. The spike of this plant is a single fertile leaf, standing in the axil of the sterile one and hence belonging to a lateral axis, of which however nothing is perceptible but this leaf. (Cf. *Schnizlein:* Icon. fam. nat., Heft II, t. 32.) The utriculus of *Carex* is the solitary leaf of an axis which in its normal condition develops no farther, and out of which, as the axillary formation of the utriculus, the female flower is emitted. And the so-called neutral flower of *Panicum*, and the related grasses, is a shootlet which develops nothing but one leaf (the bract of the flower).

ble Idea by the different members of the vegetable kingdom is precisely similar to the realization of the species by its single individuals. To be sure our idea of a plant implies that it shall manifest its life in a series of successive formations, that it shall put forth its leaves, flowers and fruit by successive steps; and yet there are plants which produce no leaves and no fruit (the Cryptogamia); again, there are others which hasten on to form flower and fruit with various intermissions of the regular steps, as is especially the case with the ugly parasites destitute of that green foliage which elsewhere is so characteristic a product of the vegetable world * One of these (the *Hydnora*,† which preys upon the root of the South African *Euphorbiæ*) seems entirely devoid of all the foliage which is usually formed before the flower. Hence, therefore, in general we cannot necessarily regard individuals as perfect representatives of the specific idea, and hence, too, we cannot regard them as representations invariably identical in their realizations. Individuals appear rather as living attempts, by which the Idea is more or less attained, and is thus realized with various modifications. From this point of view even the differences in individuals, as pointed out by the doctrine of shoots, within the limits of vegetable species will no longer surprise us; on the contrary it will open to us a deeper insight into that independence presented to us even in the life of nature, in the realization of the internal problems of the creation.

But here, too, as is so variously the case in nature, the regulative law is admirably united to the free configuration; for what gives a peculiar interest to the differences among shoots in the same species is the regular reciprocal relation among the shoots, as they reciprocally complete each other by their very one-sidedness, and thus form a higher whole. In this respect the qualitative difference of shoots bears a certain relation to their origin, that is, to the order of ramification to which they belong. And as the formation of shoots, as was shown, is a process of propagation, we see here, in the history of the development of the species, propagation taking the place of individual development. A second individual takes up the thread of reproduction which the preceding one was unable to carry any farther. Thus, what we are accustomed to see elsewhere attained in the individual, is here reached by the generation in a more or less strictly deter-

* *Orobanche, Lathræa, Monotropa, Cynomorium*, all of which agree in the inferior-leaf formation passing immediately into superior-leaf formation, and thus the formation of foliaceous-leaves is omitted. In the celebrated *Rafflesia* the immense flower is preceded by bud-scales only, which must be considered as the inferior-leaf formation. The same occurs in *Frostia*, which preys upon the branches of arborescent *Leguminosæ*, and which resembles a mere flower so much that one might doubt whether it is merely a monstrous papilionaceous flower or a real parasite. (Cf. *Endlicher:* Gen. plant., p. 76, and *Guillemin:* Nouv. Ann. des sc. nat., II, t. 1, and as to parasites in general, *Unger:* Annalen d. Wiener Museums, part II.)

† *E. Meyer:* Nov. act. acad. L. C. nat. cur. XVI, 2, p. 771, t. 58 et 59, and *R. Brown:* On the female flower and fruit of *Rafflesia* and *Hydnora*, 1844, pl. 6–9.

mined cycle,—in other words, where the single shoot is incapable, a determinate succession of shoot-series arises to bring the internal problem of its existence to a consummation,—to complete the metamorphosis into flower and fruit. This remarkable phenomenon,—which is a very frequent one in the vegetable kingdom, and is one of the essential characteristics of many of the most important families of plants, e. g., the grasses, *Synanthereæ*, *Labiatifloreæ*, *Cruciferæ*, *Leguminosæ*, etc.,—is the same as that which in the animal kingdom (in whose lower orders it re-appears) was, we cannot say discovered, but brought to a clearer comprehension not long since by the Norwegian naturalist Sars,* completed and confirmed by von Siebold's investigations into the history of the development of *Medusa aurita*,† and soon after substantiated in its universality by the Dane, Steenstrup, under the name of "alternation of generation," or propagation and development by alternate series of generations.‡ Single cases of alternation of generation had been already carefully observed:§ but they were too much in opposition to the usual mode of reproduction to be understood in their true meaning. It was attempted to reconcile them with the customary mode by an unnatural interpretation, which regarded them as subversive exceptions to the general rule; while on the contrary almost all later works‖ bring to light a multitude of unexpected facts

* In *Wiegmann's* Archiv, 1844, where the observations published in the author's earlier works, on the adolescent states of *Medusa* are completed and concluded.

† Beiträge zur Naturgesch. der wirbellosen Thiere. Danzig, 1839.

‡ Ueber d. Generationswechsel, übersetzt von *Lorenzen*, Copenhagen, 1842.

§ *Bonnet's* industrious observations, the first that were made, of the alternating mode of reproduction of *Aphis*, published in his Traité de l'Insectologie in 1745, though made in 1740, belong here. Also *Chamisso's* correct observations of alternation of generation in *Salpæ* described in his Memoir: de Animalibus quibusdam e classe vermium Linnaeana, Fasc. I, 1819. Fragments in regard to the alternation of generation of *Trematodæ* were known, (but as such they did seem very enigmatical,) by *Bojanus's* Beschreibung d. königsgelben Würmer (the "nurses" of *Trematodæ* according to Steenstrup) aus welchen Cercarien (the larvæ of the final generation) herauskommen (Isis, 1818), and by *v. Baer's* important work on *Cercariæ* and the related *Bucephalus*, (Beiträge zur Kenntniss d. niederen Thiere. Act. nat. cur., Vol. XIII, 1827).

‖ Of the later works, by which the field of alternation of generation has been extended, I will adduce in particular; *Sars:* Fauna litoralis Norvegiæ, 1846, in which the sections especially important in relation to alternation of generation are those on *Syncoryna*, *Podocoryna*, *Perigonimus*, *Cytais*, as well as on *Agalmopsis*, *Diphyes* and *Salpa*.—*Van Beneden:* Recherches sur l'embryogénie des Tubulaires (1844); Mém. sur les *Campanulaires* de la côte d'Ostende (1845 in the mém. de l'Acad. roy. de Bruxelles, T. XVII); Recherches sur l'anat., la physiol., et le dévél. des *Bryozoaires* (Mém. de l'Acad. roy. de Br. T. XVIII).—*Dujardin:* Sur le dévél. des Méduses et des Polypes hydraires (Ann. des sc. nat., Nov. 1845).—*Krohn:* Bemerkungen über die Geschlechtsverhältnisse de Sertularinen (in Müller's Archiv, 1843, p. 174); Ueber d. Fortpfl. u. Entw. der Biphoren (Froriep's neue Notizen, No. 868, 1846).—*Busch:* Beob. über Anat. u. Entw. d. Infusorien (Arch. f. Naturgesch. XV, p. 92). How great an importance must be attributed to the discovery of alternation of generation in dispelling the darkness which until then settled on the history of the life and development of *Entozoa*, may be seen in particular in *v. Siebold's* pregnant communications in *R. Wagner's* Handwörterbuch d. Physiologie, p. 640 (Article: Parasiten).

which take their places naturally under the law of alternation of generation as now known, and substantiate the pertinent words of Gœthe with which Steenstrup opens his Memoir: "Nature keeps on her course, and what seems an exception is in rule." It was Sars, however, who first gave the answer to the riddle, the key to the newly opened domain, when he said of the course of development of *Medusa*, that here "it was not the individual, but the generation, which underwent the metamorphosis."* This was the true point of view; for Steenstrup dwelt too exclusively on the physiological side, the functional relations, of the alternating generations. Steenstrup, in fact, considered that the significance of alternation of generation consisted in its being an organic nursing of the brood connected with particular generations, for which reason he termed the individuals of *these* generations "nurses;"—a mode of viewing the subject, which, with all Steenstrup's pregnant elaboration of his idea, and with all the analogies he pointed out between it and the well-known phenomena of nursing the brood by particular individuals among bees, wasps, ants and termites, does not seize the *essential* point of the phenomenon of alternation of generations † R. Leuckhardt‡ conceives alternation of generation from a more comprehensive physiological point of view, in connection with the totality of all the other phenomena of the formation of different individuals, whether it occurs in a different or in the same generation; regarding all these phenomena from the point of view of a division, not merely of the generic task, but of the vital task in general, among certain individuals; considering it as a polymorphism determined by a division of labor. But even this view must lead to the morphological one; for the division of labor is deter-

* *Sars:* l. c., p. 29. This assertion, of course, must not be understood as if the particular generation did not come in for its part of a metamorphosis. Sars' view is most beautifully corroborated by a comparison with plants; as in plants the metamorphosis of the individual itself is connected with the formation which leads to the completion of new parts, which in their turn have their own subordinate metamorphosis.

† Steenstrup's explanation is most correct in regard to the history of the development of *Distomæ*, whose nurses and grand-nurses are at last utricles entirely filled with the brood, and forming mere receptacles of the brood. Its application is less happy to those cases where the transition from the preparatory generations to the final generation takes place through *external* shoot- or bud-formation, as in *Sertularia*, *Campanulariæ*, and *Corynæ*, whose nurses forming the polypstem can continue to live even after the concluding generations, comparable to the flower in plants, separate or wither off. Hence the vital activity of the preparatory generations is not exhausted in the production of the brood. Steenstrup's view, accordingly, would only be correct if non-sexual brood-production (by internal or external shoot-formation or by division) and alternation of generation were *correlative* conditions of each other. But this is not the case, as reproduction by shoots takes place without any alternation of generation in a great number of animals (*Ascidia*, *Bryozoa*, *Madrepora*), and by division as well (*Astræa*, *Annulata*, *Infusoria*). These cases are comparable to the occurrence of *unessential* branches in plants; while alternation of generation represents the succession of *essential* shoots.

‡ Ueber d. Polymorphismus d. Indiv. od. d. Ersch. der Arbeitstheilung in d. Natur Ein Beitrag z. Lehre v. Generationsw. (1851.)

mined by the organic development, while this itself obtains its peculiar character from the determinate step of the metamorphosis at which the development ceases;—and this is just what is so unmistakable in the phenomena of alternation of generation in plants. Hence as a typical phenomenon of development, as a metamorphosis of generation, alternation of generation (as well as the metamorphosis of the individual) presents analogies with the graduated series in the animal and vegetable kingdoms, and the organic scale of the creation, in general;—a point to which V. Carus* called attention, and Reichert, his predecessor, as well.

The difficulties which the qualitative differences of shoots of one and the same species seem to present to our conception of shoots as individuals, will be entirely obviated if we can demonstrate that a partial outfit and equipment of individuals, perfectly analogous to those found among plants, are likewise found in the animal kingdom, where in most cases there is less doubt as to what is an individual,—if we can show that in both kingdoms, and in a similar manner, a polymorphism of individuals occurs which depends upon a division of the steps of development and of the vital problem of the species among individual members, whether of the same generation (divisions of generation), or of different generations cyclically succeeding each other (alternation of generation).

Let us first compare the phenomena of alternation of generation (or, as it should be called, *cyclical succession of generations*) in both kingdoms.† As is the case in the alternation of generation

* Zur näheren Kenntniss d. Generationsw. (1849); and, Einige Worte üb. Metam. u. Generationsw. (*v. Seibold u. Kolliker:* Zeitschr. f. wiss. Zool. III, 1851, p. 859).

† These remarks on alternation of generation in plants, do not depend, as one might perhaps be disposed to think, upon a zoological doctrine fancifully applied to plants. But I recognized the phenomenon as the same, and I treated of it in my papers, if not under the same name, still in the same meaning, before my attention was called to the occurrence of this phenomenon in the animal kingdom by Steenstrup's work. As soon as the doctrine of the shoot as the vegetable individual was assumed in all its consequences, a determinate succession of generations emitted one from the other necessarily appeared to be the ground of the flower's first making its appearance in many plants in a determinate degree of ramification, and of the occurrence of a determinate succession of steps in the series of axis up to this goal, caused by a peculiar partition of the leaf-formations. Hereby the essential shoot-succession, which is the one which represents alternation of generation, was accurately distinguished from the unessential one. Twenty years ago, or more, *C. Schimper* distinguished between essential and unessential shoots, denominating the first (in a wider sense of the word) "Ableger" [off-setts], the latter "Ausleger" [out-sets]. In the Versammlung d. Naturforscher in Mayence in the autumn of 1842, I made a communication on this subject, and at the same time in particular I called attention to the frequent importance of the characteristics involved in these relations when applied to improving the differentiation and grouping of species. Of this communication a report appeared in the Flora for 1842, p. 962, though, indeed, somewhat distorted by inaccuracies. *Wydler* treated the same subject in the Bot. Zeit. 1844, St. 37, under the heading "Achsenzahl der Gewächse," and gives a compendium of examples, in which, however, much appears which needs qualification. As Wydler informs us, Aug. de St. Hilaire is said to have turned his attention to ascertaining the number of essential axes in plants; however I find nothing in the place referred

of animals, a twofold reproduction appears in plants: sexual and non-sexual. Disregarding for the present the various relations of alternation of generation among the Cryptogamia, we find sexual reproduction (in animals by fertilized ova,—in plants by fertilized seeds) always vested in the generation which concludes the cycle of generations. That the consideration of this generation as the concluding one is not arbitrary, is shown by comparing it with the usual course of the metamorphosis; for the concluding generation is invested with the concluding formations of the metamorphosis (flower and fruit), in the same way in fact as in the animal the complete development of the organs of generation occurs at the summit of the individual metamorphosis. The preceding (preparatory) generations, which Steenstrup calls "nurses," on the contrary invariably produce their brood by non-sexual reproduction; in the animal kingdom this takes place, now through germ-granules which develop in the interior of the body (as the nurses of Distomæ), now by a process of division in the posterior part of the body (the nurse of the *Medusæ*, the *Tapeworm*), or finally by external, persistent or deciduous, shoot-formations, (*Corynæ*, *Campanulariæ*, *Sertulariæ*, etc.). Among Phanerogamia the last is the only kind occurring subservient to alternations of generation.

In animals, as in plants, the number of the generations in which the cycle of alternation of generation is completed, is for the most part a determinate one. *Medusæ*, *Salpæ*, *Corynæ*, *Tubulariæ* conclude this cycle in the second generation; according to Steenstrup's showing, *Distoma pacificum* has a trimembral alternation of generation, and the family stock of *Pennatula* seems also to be formed by a trimembral succession of shoots. *Campanularia* has a quadrimembral cycle, in which however the two first generations are of the same character. Among *Sertulariæ* cycles of still more numerous members appear to occur; eight to ten generations form the annual cycle of generation of *Aphides*, though, excepting the last one, they are all similar and not even determinate as to number.

To these examples from the animal kingdom much more numerous ones from the vegetable kingdom might be added, though

to in the *Leçons de Botanique* but the distinction between determinate and indeterminate growth, which has been known since Joachim Jung's time, and was brought forward especially by Rœper and applied by him to classifying infloresences. It is exemplified, in that place, by creeping stems, upright root-stocks, and by bulbs; and the section on indeterminate stems is unluckily exemplified by wrong cases, viz., *Scirpus palustris*, *Primula officinalis* and *Menyanthes*, to which indeterminate main-shoots are falsely ascribed.—Steenstrup, also lays down an alternation of generation in plants, in the concluding remarks in his work quoted above, as well as in his later book, "Ueber das Vorkommen des Hermaphroditismus in der Natur," (On the phenomenon of hermaphroditism in Nature), though in an entirely different manner from mine as here given, for he compares the single leaves of the plant with the individual in animals,—a mode of viewing the subject in regard to which I have already expressed my opinion in the Introduction.

I will only adduce a few of them here. Most *Labiatifloræ*, *Synanthereæ*, *Grasses*, *Polygaleæ*, *Primulaceæ*, the *Dictamnus*, *Iris*, *Galanthus nivalis*, etc., have a bimembral alternation of generation in different ways, according to the partition of the formations. In *Paris*, for example, the first generation takes the lowest grade: it presents a subterranean inferior-leaf shoot, (rhizoma) which never leaves the darkness of the earth, only reaching the world of light, towards which all plants strive, in its posterity, viz., in the quadrifoliate and unifloral lateral shoots which it sends up. The first generation of *Viola odorata* and related species forms foliage proper; still, the main axis tarries close to the earth, and the second generations (the lateral flowers) scarcely rise above the foliage. In *Lysimachia nummularia*, the main-shoot, a rooting leaf-stem, creeps along the surface of the ground, growing indefinitely, and terminating only in the (essential) lateral branches by its golden-yellow flowers. The main shoot rises perpendicularly, forms foliage proper, and passes on to superior-leaf formation in many species of *Veronica*, e. g., *V. acinifolia*, producing its flowers as a second generation out of the axils of the leaves. The same holds good in regard to *Orobanche ramosa*, which fixes itself and preys upon the root of hemp, though its main-shoot has no green leaves. A very remarkable bimembral alternation of generation is shown by *Adoxa*, now so famous, its name to the contrary notwithstanding.* The main-shoot creeps along the ground, oscillating with the seasons between leaf- and inferior-leaf formation,—at every return of the latter stretching out like a runner and boring into the earth. Flowers and fruit, frustrated by the invariable retrogression of the main-shoot, are produced by the aspiring perpendicular branches, after a pair of small leaves on the scape, and several insignificant superior-leaves, out of whose axils the lateral flowers are emitted as unessential shoots of the third degree. *Hepatica* presents a similar division of the formations among the two generations of shoots; but the main-shoot, rejuvenated from year to year and alternating between inferior-leaf and leaf-formation, is short and upright. The branches with their single flowers, forming the second generation arise in the axils of the scale-like inferior leaves. A bimembral succession of shoots occurs in *Convallaria*, *Polygonatum*, the genus *Alœ*, all species of *Plantago*, *Veronica officinalis*, *Chamædrys*, etc., *Viola sylvatica*, *Lysimachia thyrsifolia*, *Alyssum saxatile* and some other *Cruciferæ*, *Echeveria coccinea*, all the species of *Melilotus*, *Medicago*, *Galega*, in *Pisum*, and many other leguminous plants, and in *Succisa pratensis*, *Anacyclus*, *Pyrethrum*, *Polygonum Bistorta*, etc. A familiar example occurs in

* E. g. *Adoxa moschatellina*, which derives its name from δόξα (fame). The relations of growth in this plant have been correctly described by *Wydler*: Bot. Zeit. 1844, p. 657.

Secale. Its spiciferous culm forms the shoot of the first degree, the lateral spikelets which compose the spike itself are those of the second,* and the florets in the axils of the superior leaves (paleæ) of these spikelets are the shoots of the third degree, i. e., the third generation of the cycle. A quadrimembral succession of shoots occurs in *Trifolium montanum*, *Hedysarum coronarium*, and in several of the New Holland phyllodineous *Acaciæ.* Several species of *Carex*, e. g., *C. maxima* and *leptostachys*, have a trimembral succession of shoots up to the male flower and a five-membral one up to the female.

If we were to reckon the similar generations which are reared one above the other until the tree gains strength enough to perfect its flowers, in many trees without terminal buds, as, in the Willow, the Linden,† we might find a number of generations equal or even much superior to that presented by *Aphis.*

Besides the generation *essential* to itself, and by which it gives existence to the next grade in the cycle, every generation can have still another unessential reproduction, which only extends the same grade. As above we distinguished between essential and unessential shoots, so here accordingly we must distinguish an essential succession of generations,—the true alternation of generation,—and an unessential one. Very often both occur in the same species of plants. A fine example of this is shown in *Lysimachia nummularia*, from whose creeping and rooting leaf-axis are emitted not only peduncles, but here and there new creeping leaf-axis exactly repeating the original one (except as to the two early-lost cotyledons): and from the undetermined leaf-bearing main-axis of *Tropæolum minus* are emitted in regular alternation three lateral flowers at a time, and then again one (unessential) leaf-shoot. In *Cardamine amara* the first generation (the stem bearing foliaceous and superior-leaves) is repeated in a twofold manner, by lateral branches from the cauline leaves, and by creepers from axils of the root-leaves. Similar relations obtain in *Mentha* and a large number of other plants. This same phenomenon is repeated in the animal kingdom. The polyp-like nurses of the *Medusa* increase as such (according to Sars and von Siebold) by lateral buds and runners. *Syncorynæ* are spadix-polypi, which represent trees by their formation of unessential branches, emitting finally from every branch and from the middle stock a whorl of individuals of the second (and last) degree. *Campanulariæ* and *Sertulariæ* put forth runners from the bases of the main-individual, which again shoot up and become new main-stems, or new stems emerge out of them; and perhaps the

* *Secale*, in fact, has no terminal spicule; neither has *Triticum monococcum*, while the other cultivated species of *Triticum* have.

† I have described the grape in reference to this subject in another place, (Verjüngung, p. 49,) [*Henfrey's* Transl. op. cit. p. 46. T.].

ramifications of *Bucephalus* (which according to Steenstrup's supposition is the larva of *Aspidogaster conchila*) as represented by Baer in Nov. Act. Nat. Cur., xiii, 2 belong here.

In our qualitative comparison of shoots, it was shown how the shoot can be limited to a few leaves, or even to a single one; in like manner the animal individual, in the division of *rôle* which occurs in alternation of generation, can become the representative of one single organ, of one single function. Thus the females of *Coryne squamata* are hardly anything more than egg-stocks, and the males than seed-stocks.* The members of the *tapeworm*, which are so many individuals of the final generation, hardly represent anything more than hemaphrodite sexual apparatus. As an analogous example in the vegetable kingdom perhaps the *Willow*† may be compared to the *Coryne;* here too the shoots of the last degree are nothing but naked unisexual apparatus of reproduction. In *Potamogeton*,‡ on the contrary, they are hermaphrodite, as in the tapeworm. The construction of many of the lower animals, which when considered as individual animals seem to be the strangest monsters, becomes more intelligible as soon as they are regarded from this point of view, —as soon as we make up our minds to regard the supposed individuals as a family stock, and its parts (formerly held to be mere organs, and which, physiologically considered, are really nothing more) as individuals. In particular this is true of *Physophora Stephanomia* and *Agalmopsis.*

In many cases we find alternation of generation connected with division of generation, that is, the appearance of heterogeneous individuals in one and the same generation. Just as is the case in animal and vegetable forms without alternation of generation, so where it is connected with alternation of generation, division of generation relates principally to the sexual functions; and a glance at the animal kingdom shows us relations of alternation of generation complicated by division perfectly similar to those which occur in the vegetable kingdom. In animals which go through an alternation of generation the individuals of the preparatory generations are non-sexual; still they may nevertheless have a determinate importance in relation to the completion of the race which is to form their posterity. When in fact the final generation does not consist of hermaphrodite individuals, as obtains, for instance, in the tapeworm, various alternations are conceivable: the final individuals of both sexes can be nourished by the same nurse, and hence the sexual division will first take place in the second, or generally speaking, in the last generation;

* Hence *Rathke* regards the male individuals as mere testicles. Cf. *Wiegm.* Archiv., 1844, p. 155, and *Steenstrup:* Hermaph., tab. I, f. 17–20.

† The two stamens in the Willow, and the floriferous bud as well, is preceded by only two very small bracts, which grow together and form a little scale.

‡ The flowers of *Potamogeton* are branches which bear only stamens and carpels.

or, different nurses may nourish the two sexes so that a division of generation will occur even at the degree of nurse-formation. If in the last case the nurses are not single ones, but even then form *per se* a family stock, then on the same stock we may either have male-bearing and female-bearing nurses together, or these two kinds of nurses may be divided among different stocks, according as the division of generation occurs in a determinate later generation, or is present already in the first. Although as yet the observations of these relations by no means form an unbroken chain,* still this much is certain, that in animals, in the same way as in plants, both monœcious and dœcious forms occur; and hence there are families partly bisexual, partly unisexual. *Corynæ*, *Tubulariæ*, *Campanulariæ*, and probably all *Sertulariæ* (hence, doubtless, the greater part of *Hydroids*), also *Veretillum*, *Cynomorium*, according to Steenstrup, Krohn and other observers, are diœcious,—whether they form small simple stocks as *Coryne squamata*, or small ramified trees, as *Syncorynæ*, *Campanulariæ*,† etc. On the other hand *Siphonophoriæ*, according to Milne Edwards' description of *Stephanomia*‡ (and judging from Sars' description of *Agalmopsis*), are monœcious family stocks; Hydræ are also monœcious.§ To enter any further into these relations as they occur in the loweranimals would lead us too far from our subject; but it may be in place to give some details as to the manifold relations under which sexual division of generation occurs in plants.

Diœcious relations may occur without alternation of generation when, in fact, the flower has a terminal inflorescence and no branches, or only unessential ones,—when, therefore, as it is usually expressed, it is "uniaxial," as e. g., in *Rubus*, *Chamæmorus*, *Lychnis*, and *Viscum*. Much more frequently, however, division of the sexes occurs in plants which at the same time have a cyclical succession of shoots (alternation of generation),—a succession which each of the two heterogeneous stocks passes through independently, and not always *pari passu*. This is a circumstance which must not be neglected in considering the differences of *habitus* in male and female flowers. Thus, in *Mer-*

* Thus e. g., as far as I know, it remains to be shown whether the single nurses of *Medusae* produce *Medusae* of both sexes, or, as is most probable, only those of the same same sex. In *Aphis* also this point still needs to be more accurately determined.

† *Steenstrup:* Hermaph., pp. 66, 67, 72.

‡ Ann. des Sc. Nat., 1841, p. 217, pl. 7–10.

§ The later investigations into *Siphonophoriæ* by *Huxley:* Edin. Phil. Journ., 1852, *Kölliker:* Zeitschr. f. wiss. Zool., 1852, and *Leuckardt:* Zool. Untersuch., 1stes Heft, 1853, corroborate the monœcious relations of these wonderful creatures as regards most of their genera, e. g., *Agalma*, *Agalmopsis*, *Stephanomia* (*Apolemia*), *Physophora*, and the other closely related genera; *Busch's* researches into the group of *Diphyidæ* have proved them to be diœcious, and the same obtains in the related genus *Epibulia*. (Later note.)

scuriali the female plant bears flowers even on the second axis; in the male plant, however,—if I do not misunderstand the inflorescence (a spike composed of small glomerules)—this first occurs on the third. In *Carex dioica*, vice versa, the male plant, flowers in the second line and the female in the third.* In other diœcious plants on the other hand, the male and female flowers appear in the corresponding generation, e. g., in the second: *Stratiotes*, *Empetrum* and *Tax*nen in the third: *Salix*, *Populus*, *Myrica*, *Cannabis;* in the fourth: *Phœnix.* In Hemp the extremely heterogeneous appearance of the inflorescence of the male and female plants does not depend upon a division of the flowers of the two sexes among different axes, but upon the production of numerous unessential peduncles in the male inflorescence.†

Monœcism necessarily presupposes a succession of shoots (alternation of generation); in the simplest case at least for one of the two sexes, as both cannot be united in the same terminal flower: but *vice versa*, both may easily appear in determinate (equal or unequal) degrees of ramification. The most important circumstance to be considered in monœcious relations, consists in both the sexes (i. e., the shoots which bear them) occurring either subordinately or coördinately,‡ for one either arises out of the other, or they both spring from a common mother-stem. In the first case, the female flower usually belongs to the earlier, the male to the later (subordinate) generation; the male flower-shoot springing from the female,§ as e. g., in *Euphorbia*, *Ricinus* and *Poterium*, in which the female flower terminates the main axis, and the male occurs as a lateral shoot.‖ In *Buxus* the female flower occurs as the second, the male as the third axis; in many species of *Phyllanthus* (e. g., *Ph. niruri*) the female as the third, the

* The second axis, which is a complete dwarf or a mere bristly spine bears the so-called Urceolus, in the axil of which the female flower is placed, as the third member of the succession of generations.

† The female flowers are placed at the sides of the primary branches as branches of the second degree. In the same place where one single flower occurs in the female plant, a furcately ramified inflorescence is found in the male, produced by branching out of the two bracts of the original flower.

‡ Both these cases doubtless occur in the animal kingdom, the first probably in *Alcyonella*, where the stock is said to be composed partly of males and partly of females. As the stock is here formed by individuals continually shooting out of each other, one sex must shoot out of the other. The second case occurs in *Agalmopsis* (according to Sars,) where partly female (seminal vesicles,) and partly male individuals grow out of the same main-stem.

§ The opposite case seems to occur very rarely or not at all. A monstrosity, which, for some reasons might be adduced here, is found in *Larix Europæa* and *Picea alba*, in which transitions of the amentaceous male flowers into female cones occur, where the fruit scales are emitted from the axils of stamens which are often only slightly abnormal.

‖ As in all the examples adduced, the unessential aggrandizement of the inflorescence must be disregarded, which occurs in *Ricinus* and *Poterium* in the form of lateral female flowers emitted beneath the terminal female flower.

male as the fourth ; in *Xylophylla*, the female (on the margins of the spurious leaves) as the fourth, the male arising from the bracts of the female flower, (as in *Phyllanthus*) as the fifth. In *Momordica*, *Echalium*, *Cephalanthera* and some other *Cucurbitaceæ*, the female flower, placed in the axils of the foliaceous leaves of the main stem, belongs to the third axis, and the male to the fourth ; for the third axis, which here arises from the base of the peduncle of the female flower as main axis of the racemose male inflorescence, is a superior leaf-shoot. In the other cases,—in which the succession of shoots, in order to arrive at the two kinds of flowers, separates into two cöordinate lines,—both kinds of flowers can appear either immediately in the first generation after this separation, or, since here again preparatory generations are intercalated, in a later one. Further, the number of the generations (axes) in the two lines arising from the division, may be either equal or unequal. A few examples may serve to explain the manifold cases which thus occur. In *Musa*, *Myriophyllum* and *Sagitaria* the coördinate male and female flowers appear in the first generation after the separation, and in the whole as a second system of axes. Here the female flowers stand in the lower, the male in the upper part of the spicate or racemose inflorescence. The contrary holds true of *Cucurbita* and the monœcious *Bryoniæ* ;* for here the earlier flowers, which appear in the axils of the foliaceous leaves, are male ; while the later ones which appear on the farther continuations of the stems are female. *Arum*† has below female, in the middle male, and above again female flowers, though these last are dwarfed and sterile. Likewise in the first generation after the separation, but in the whole as the third system of axes, we find both kinds of flowers in *Pachysandra* and *Acalypha*, and here again, as is usually the case in indeterminate spicate inflorescences of mixed sexes, the female flower is in the lower, the male in the upper part of the inflorescence. The same obtains in monœcious Palms with axillary spadices ; though here the flowers appear in ramified spikes from the fourth system of axes. When the flowers make their appearance in the second generation after the division, they cannot easily be united in the same inflorescence, and special male and female inflorescences will arise. Thus, e. g., in *Platanus*, *Liquidambar* and *Sparganium*, in which the female inflorescences occur on the lower part of the main shoot, and the male in the upper ; likewise in *Quercus* and *Fagus*, though here, *vice versa*, the male inflorescences are the lower, and the female the upper. Finally,

* *Bryonia* has apparently axillary racemes, but a more careful investigation shows that they do not spring immediately out of the axil of the foliaceous leaf, but (as secondary branches) out of the peduncle of a single flower standing directly in the axil of the leaf which exactly corresponds to the flower in *Cucurbita*.

† The inflorescence in *Arum* is terminal, as well as that in *Calla*.

if the division of the succession of shoots is an unequal one in the separated lines of generation leading to the two kinds of flowers; i. e., if the number of essential axes is unequal, it is greater sometimes for one sex and sometimes for the other. In the Walnut (*Juglans*) it is the male flower which attains the higher degree of ramification; in *Xanthium* and the species of *Carex* with separated male and female spikes it is, on the contrary, the female flower.*

Other dimorphisms or even polymorphisms of the flowers, more or less independent of sex, occur when the sexes appear in the two different lines of generation; for even among flowers of the same sex, whether hermaphrodite, male, or female, differences often reveal themselves of a very striking character, which are generally coördinate according to fixed laws of division of generation. Thus, in all *Primulæ*, and in several *Labiatæ*, two kinds of hermaphrodite flowers occur, in a state of diœcious separation: one with a large corolla and strongly developed stamens (*forma brevistyla*), the other with a small corolla and strongly developed pistils (*forma longistyla*). Acccording to C. Schimper's observations† both forms occur at times in *Labiatæ* even on the same stock and in the same inflorescence, e. g., in *Dracocephalum Moldavica*. Many species of *Viola* also produce two kinds of hermaphrodite flowers on the same stock: early ones of the usual form, and late ones without petals. In *Viola mirabilis* the first arise directly out of the main stem (as branches of the first degree) and are mostly sterile, while the latter spring from the foliaceous branches (as branches of the second degree) and are fertile. In *Impatiens* sterile flowers with perfect corollas and apetalous fertile ones occur in the same raceme. The cases in which normally formed above-ground and abnormally formed underground flowers appear belong here; the latter have their corolla developed slightly or not at all, and are merely female, and, *par excellence*, fertile. If both kinds of flowers are fertile, the subterranean fruit differs from that borne above the soil; such cases are found especially in the family of *Leguminosæ*, e. g., in several species of *Lathyrus* and of *Vicia*, in *Amphicarpæa*, and in *Arachis*;‡ and also in the very remarkable Abyssinian *Con-*

* In species of *Carex* with terminal male and lateral female spikes, the male flower belongs to the first generation after the division, and the female to the third. In most of the species where the shootlet which bears the inflorescences is a continuation of the main axis of the plant, the male flowers represent in general the second generation and the female the fourth; in those species, on the other hand, which have a shortened main axis, which forms a mere rosette of leaves whence the shootlets bearing the inflorescences proceed as branches,—in these species the male flower is the third system of axes, and the female the fifth; as e. g., in *Carex maxima*, *leptostachys* and *pilosa*.

† Communicated in the Versam. d. Natur. zu Wiesb. in Sept. 1852.

‡ For details, vid. *Treviranus:* Bot. Zeit., 1853, p. 393.

volvulacea, *Hygrocharis Abyssinica*.* Among the most striking cases of dimorphous flower-formation are those described by *Jussieu*† in *Gaudichaudia*, *Camarea*, and other *Malpighiaceæ*. Here, besides the flowers conjoined in racemes or in corymbs, and formed according to the common type of the family, other apetalous flowers occur, standing alone and hid in the axils of the leaves. Besides the normally formed glandulose corolla, they have only one stamen and two carpels. In several cases the dimorphism of the flowers is confined to the formation of the fruit alone, as, e. g., in some species of *Æthionema*, (especially *Æ. heterocarpum*, Gay,) which in the same raceme bear partly dehiscent silicles with two cells and several seeds, and partly one-celled and one-seeded indehiscent silicles. *Ceratocapnos*,‡ a North African genus of *Fumariaceæ*, bears in the lower part of the spike oval, ribbed, one-seeded nutlets, and in the upper part, lanceolate two-valved and two-seeded siliques. Polymorphism of flowers and fruit occurs in the most heterogeneous manner in the family of *Compositæ;* I will only refer to *Zinnia*, *Dimorphotheca*, *Heterotheca*, *Thrincia*, *Geropogon*, *Crupina;* and especially to *Calendula*, where the hermaphrodite blossoms of the ray produce three different forms of fruit, so that, including the male flowers of the disc, the capitulum presents four different forms of flower-shoots (belonging to the same generation). As somewhat similar cases in the animal kingdom, the instances of dimorphal insects, of which there are several, might be adduced.§

A separation of the series of generations into several distinct lines occurs in fact not only as regards the flower, but also, though less frequently, even among the inferior formations of the plant; this is especially the case where a particular lateral line is allotted to the leaf as well as to the flower. The true Pines afford the best known example of this. Their fascicles of needle-shaped leaves are nothing but foliaceous branches of circumscribed growth,‖ which lie outside of the line which leads to the two kinds of flowers, while they are essential as the leaf-formation

* *Hochstetter:* in Schimp. Iter Abyss., No. 572 et 1701. The same plant is called *Nephrophyllum Abyssinicum* by *Richard:* Tent. Flor. Abyss., and figured in pl. 76. The two kinds of flowers are emitted from the axils of the foliaceous leaves of the same creeping stem; those provided with corolla, stamens and pistil stand upright; the others without corolla and stamens, bend down to the ground on their long peduncles.

† *Adr. de Jussieu:* Monographie des Malpighiaceés. (1843.)

‡ *Durieu:* Explor. scient. de l'Algérie, pl. 78. *Endlicher:* Gen. plant., Suppl. IV, p. 32.

§ The first in several species of *Dyticus* (*D. marginalis, circumcinctus, Lapponicus, Rœselii*, according to *Erichson:* Gen. *Dyticeorum*, 1832, p. 31; the last in *Aphis Quercus* according to *Bonnet.*

‖ That the fascicles of leaves in *Pinus* are branches, is proved by the phenomenon of percrescence, which is not unfrequent, especially in young pines.

appears on them alone.* Here the generation splits up into three kinds of essential and coördinate shoots: 1st, the small leaf-shoots which after some few inferior-leaves forming the vagina, bear two, three, or five foliaceous leaves; 2d, the male flowers, or small shoots, which are provided with stamens only; 3d, female inflorescence, shoots with superior-leaves (the integumentary scales of the strobile) in whose axils the fruit-scales of the cone are formed, belonging to a farther system of axes. In the animal kingdom cases analogous to these occur in monœcious *Siphonophoræ*, especially in *Stephanomia* and *Agalmopsis*, where even more than three kinds of coördinate individuals are emitted from the main axis: in particular motory individuals (the so-called *swimming-bells*), nurses, the proboscis-like formations or imbibing tubes, and as already mentioned, two kinds of sexual individuals.

The differences of shoots thus far considered depend principally upon this: one portion represents exclusively the vegetative formation, or a certain part thereof; the others represent the degrees of formation which belong exclusively or principally to the sphere of fructification. Hence, in regard to the division of functions, to one portion the functions of nutrition are allotted, to the others those of generation. For this reason the different kinds of shoots of such a partial character must unite in a determinate succession, and complete each other; and even those which we have designated as unessential are of importance in enriching, preserving, and increasing the plant-stock. Finally, we have still to consider those shoot-formations which properly do not belong either to the essential or the unessential succession of shoots, but rather to an *aberrant* formation; as they neither conduce to the perfection of any of the common steps of the metamorphosis, nor perform any essential physiological function in the plant, but at the best are only of some service as organs of defence, support or adherence. These are the shoots which take the form of thorns, bristles, hooks and tendrils, which for the most part owe their peculiar abnormal character to an entire suppression of the leaf-formation, and a final induration of the point of vegetation: these seem to be the last, terminal or lateral members of the generation, abortive in every respect. Not unfrequently they form the last ramification of paniculate and dichotomous inflorescences, like terminal flowerless peduncles, as, e. g., in *Teloxys* (*Chenopodium aristatum*, L.), *Acroglochin*, and in a very peculiar form, branching and complicated by aculeate or setiform leaf-formations, in *Pupalia*, *Desmochæta*, *Digera* and

* The main-stem, as well as all the elongated branches essentially resembling the stem, bear only leaf-scales, which may be best compared to bud-scales, and ascribed to the inferior-leaf formation. It is only in early youth (in the first and second years) that the main-stem itself bears needle-shaped leaves.

Cometes;* also, in *Scleropus*, where they take the form of short, thick, cartilaginous stalks, with two converging leaf-apicules. Among the grasses they are known under the form of bristles in *Setaria*. In many Rhamnaceous and Sapindaceous plants (*Helinus*, *Cardiospermum*) they appear as small cirrhi. not as the last sterile ramifications of the inflorescence, but on the contrary as the first, followed by other fertile peduncles. They often occur in the axils of foliaceous leaves; and wherever they make their appearance they naturally arrest the farther succession of shoots, when they have neither of the two leaves at their origin, out of whose axil an additional shoot may be developed. This is the case in *Passiflora*, whose flower arises from the axil of a leaf situated at the side of the base of the tendril. The thorns of *Ononis*, *Elæagnus* and *Maclura*† present the same phenomenon. In other cases the succession of generation thus arrested by the aculeate shoot is restored by secondary formations; when, with the thorn, a second shoot follows out of the axil, which in some cases may form a leaf-shoot, and in others a flower-shoot. This happens in *Gleditschia*, in several *Acaciæ* (e. g., *A. pulchella*), in *Prinsepia utilis*,‡ the Lemon, the Egyptian *Balanites*, *Duranta*, *Bouganvillea* and *Randia*, in which the secondary shoot arises close under the spine; while in *Celastrus pyrrhacantha*§ and *Europæus*, as well as *Pisonia aculeata*,‖ the secondary shoot occurs above the thorn. In *Uncaria pilosa*¶ and *Strychnos spinosa*, pairs of leaves with axillary thorns alternate with pairs which have peduncles in their axils.

Have even these phenomena of extreme alienation of the individual (as they occur in the thorns and hardened shoots of plants) analogous forms in the animal kingdom? Yes, I believe they have! I believe I may assert that in the animal kingdom itself there are individuals which occur as mere fixed claws, pincers, scourges, tactual and predial filaments, etc.,—individuals which perform neither functions of nutrition nor of reproduction in the society to which they belong, but which probably merely assist in seizing the food, or lend a helping hand in defending the community. The cases which I have here in mind are of frequent occurrence among Bryozoa, and especially in the group

* The plumose tails which form the "envelope" of *Cometes*, are the last branches of the dichotomous inflorescence, accompanied by similar accessory (secondary and tertiary) branchlets. All these numerous sterile branchlets are elongated and beset with setiform leaflets arranged in spiral order ($\frac{2}{5}$), commencing with two similar anterior leaves. The direction of the phyllotaxis in all these branchlets follows the law of furcate inflorescence.

† Here belongs also the curious hook of *Uncinia*, which is also visible, though less developed, in many species of Carex. The utriculus is a leaf at the base of this spine.

‡ *Boyle:* Illustr. of the Bot. of Himal., pl. 38, fig. 1.

§ *Boissier:* Voy. bot. en Espagne, t. 38.

‖ *Rheede:* Hort. Malab., vii, t. 17.

¶ *Wallich:* Plant. As. rar., t. 170.

of *Cellariæ*. Individuals in the form of horns (which usually conclude the series of complete cell-inhabiting individuals) occur, e. g., in *Eucrabea cornuta*,* and *Cordierii*;† in another form (reminding us of *Teloxys*,) as forked terminal spines, in *Vesicularia spinosa*.‡ Moveable individuals, representing mere weapons, in form like a bird's beak, a crab's claw or a pincers, appear in *Acamarchis avicularia*§ and *flustroides*,‖ *Retepora cellulosa Scrupocellaria scruposa*¶ and many others. In the last named *Cellariæ*, besides the claw-individuals, there are also scourge-individuals, which Van Beneden himself compared to the cirrhi in plants, and which even Leuckardt** acknowledges to be individuals. Beside the 'Swimming-bells' evidently resembling *Medusæ*, the peculiar retractile predial filaments of the *Siphonophoræ* doubtless belong here also; they are remarkable for a purplish-red swelling on or under the apex, and they shoot out singly as branches from the stalk of the nutritive individual (imbibing-tubes), and themselves bear a series of similarly formed filaments as secondary branches. They are found with unimportant departures from this form, especially in *Physophora*,†† *Diphyes*‡‡ and *Agalmopsis*. In the last named genus, according to Sars,§§ they have even three modifications: the spadiciferous terminal piece ends in a long simple filament, or in a short two-parted one, or without any filament at all. In *Stephanomia*‖‖ numerous filaments, called tentacles, arise out of the stalk of the nutritive animals (the so-called proboscis-formed organs) without such colored swellings, which in the same manner may also be regarded merely as individuals with a very incomplete outfit of organs.¶¶

* *Ellis*: op. cit. pl. 21, f. 10. (*Cellaria cornuta*); *M. Edw.*: Ann. d. Sc. Nat., (1838) t. 8, f. 2 (*Crisidia cornuta*).

† Déscrip. de l'Eypte: Polypes, t. 13, f. 3.

‡ *Van Beneden*: Rech. sur les Bryozoaires, t. 4, f. c.

§ *Van Beneden*: l. c., t. 6, f. 1–8 (*Cellularia avicularia* Pall. *Crisia avicularia* Lamx.)

‖ *Ellis*: op. cit., pl. 38, f. 7.

¶ *Van Beneden*: l. c., t. 5, f. 8--16 (*Cellaria scruposa* Auct.)

** *Leuckardt*: Polymorphism. p. 17.

†† *Philippi*: Müller's Archiv, 1843, taf. 5.

‡‡ *Sars*: Fauna lit. Norw. tab. 7.

§§ Ib. tab. 5.

‖‖ *Milne Edwards*: Ann. d. Sc. Nat., 1841, pl. 7--10.

¶¶ Since Sars observed the separation of the Medusa-like sexual individuals in *Agalmopsis*, the view that *Siphonophoræ* are composite animal stocks has gained ground more and more among zoologists. But this mode of viewing the subject was for the first time carried out (after a fashion,), consequently in Leuckhardt's latest work on strange animal forms (Zool. Unters, erstes Heft: Siphonophoren, 1853); and this idea had forced itself upon me as early as 1847, when I compared the description *Diphyes* with *Agalmopsis*, in Sars' Fauna lit. Norw. In the above named work, Leuckhardt extends the view which allows individual importance to the parts of the stock of *Siphonophoræ* not only to the tentacles and predial filaments, but also to the covercles, which in most of the genera are placed close above the nutritive individual as protective envelopes; these formations, like all the other appendages of individual importance, being emitted from the stem as shootlets, and in the first stages of their formation, resemble the tentacles in particular. Accordingly *Siphonophoræ* have not less than *eight* different forms under which the individual may appear on the whole stock. . . . (Later note.) [I have omitted the enumeration of these forms.—T.]

After having in the foregoing review regarded all lateral shoots which spring from the main axis of the plant as real individuals, however unimportant a fraction of the total specific character they may realize, it will hardly be deemed surprising if we finally apply this mode of view to the *branches of the root* and to *adventitious shoots*. It is only possible for the main-shoot to develop freely both the points of vegetation of the axis; yet even here the lower point remains undeveloped. On the contrary, the lateral shoots, thus far considered, have no lower point of vegetation; for their base is united to the maternal shoot, and hence they are mere developments of the upper point of vegetation. Opposed to these, there are, however, other shoots by which the lower point of vegetation is represented, and which on the other hand have no upper point of vegetation. Among these may be reckoned not only the root-branches which take their rise from the main root, but also all adventitious roots which spring from the stem at determinate or indeterminate places. I must, however, content myself with this general hint, as any attempt to particularize these relations could after all only show the deficiency of the investigations into this subject, and how desirable a more comprehensive work is on root-formation in the vegetable kingdom.

The few points which I have selected out of the inexhaustible field of shoot-formation in the vegetable kingdom may in the mean time suffice to show that the comparison of the vegetable shoot with the animal individual is not far-fetched or arbitrary, but is presented to us by Nature herself. The solution of the difficulties which this mode of conceiving the vegetable individual encounters in the lowest grades of the vegetable kingdom, I must defer to a later day. These difficulties are founded upon the less complete organization of the inferior plants, and at all events, cannot invalidate the results gained in considering the higher organizations. We may therefore consider it settled, that although the individual has not exactly the same importance in the vegetable kingdom as in the animal, plants still realize their vital cycle in sections which are not only comparable to the animal individual, but are in fact its complete analogues. What distinguishes plants is the formation of family-stocks, (a formation manifested in the highest vegetable representations, and here in the richest fullness),—as ancestral trees organically connected, variously disposed in their ramifications, and comprising numerous generations, rendered reciprocally complete through individuals variously endowed. And this leads us back again to the tree from which we set out; in which even our natural perceptions seemed to discern something more than one common individual, and whose high import scientific research must confirm. Just what at the outset appeared to be an obstacle to our allowing the single

shoots of the tree their true significance,—now that we have compared them with alternation of generation in animals at length proves to be the most conclusive demonstration of the correctness of our first conception. The conception of these so heterogeneous shoots as individuals of one and the same species has led us, in fact, to a more profound and more pregnant conception of individuality, which will no longer seem paradoxical when we perceive it is confirmed even in the highest realms of life—in the sphere of the mental development of the individual. Or are the differences of human individuals in mental endowment and development less important than those which we have seen in the morphological and physiological endowment and development of shoots? Do we not meet with a similar reciprocal completion, a similar division of labor among the individuals of the family, of the state and of nations, and cannot even the human individual become likewise a mere organ? Do we not see the development of the human race itself bound up with a succession, in which the later generations continue the edifice their predecessors began, like branches depending upon the earlier stocks and nourished by them;—in which generation is added to generation, and cycles to cycles; so that thus by the ever-renewed labor of the individual the problem of human life may be ceaselessly aspired to, and at last reach its final accomplishment?*

* The preceding pages were almost all printed when I was fortunately enabled to read Reichert's memoir (die monogene Fortpflanzung, Dorpat, 1852,) upon a subject closely allied to the one here discussed. His work is full of new views of the subject, elaborated with great acuteness. The vegetable individual itself is considered in detail, and the author is thus led to a mode of viewing this subject similar to the Schultz-Schultzenstein-ian doctrine of *anaphyta*—regarding not only the shoot, but even its single parts, the internodes, with their leaves, as series of individuals shooting out of each other, or intimately connected by continuable bud-formation. Since, however, it is implied in the idea of an individual, that it shall somehow be limited by, and distinguishable from, (notwithstanding it is connected with) others; it seems to me that even from this point of view Reichert's idea can by no means be carried out. I will not deny that there are still other considerations in the nature of the shoot which it is difficult to reconcile with the idea of the simple individual, and I can only find the ground of this phenomenon in the fact, that the individual appears in its full import in the higher steps of the series of created beings, while in the lower it loses more and more its reality, if I may so say. I must reserve farther remarks on this subject until I treat of the individuality of the lower plants.

[We cannot but think, after all, that this view of Reichert's, &c., which our author rejects, is the legitimate conclusion, to which the very line of argument so completely and ably presented in the preceding pages, when fully carried out, naturally leads. It is merely a question of *degree* of individuality. As yet, perhaps, no sure middle ground has been secured between the two extreme views,—one of which regards all the vegetative offspring of a seed, however numerously multiplied, as philosophically the individual; while the other views the phyton, or in the simplest lower plants the cell, as philosophically representing the individual,—real individuality being incompletely realized (and with various grades of incompleteness) in all vegetables, and in many animals. The mind is reluctant to accept either of these conclusions, and seeks—thus far in vain—for some stable intermediate view. Of the two extreme views, if forced to the choice, we should incline to prefer the latter.—A. G.]